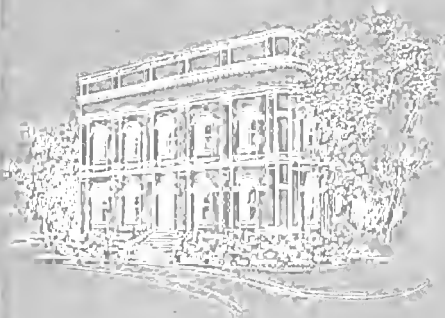


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Volume 109
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CONTENTS OF VOLUME 109, NUMBER 1

PROCEEDINGS

RAYLENE COOKE, ROBERT WALLIS, ALAN WEBSTER AND JENNY WILSON Dict of a family of powerful owls (<i>Ninox strenua</i>) from Warrandyte, Victoria	1
MARGARET C. WARK Regeneration of some forest and gully communities in the Angahook–Lorne State Park (north-eastern Otway Ranges) 1–10 years after the wildfire of February 1983	7
G. R. SHI AND SHU-ZHONG SHEN A Late Permian brachiopod fauna from Selong, southern Xizang (Tibet), China	37
THOMAS A. DARRAGH Gastropoda, Scaphopoda, Cephalopoda and new Bivalvia of the Paleocene Pebble Point Formation, Victoria, Australia	57
ALEXEI SMIRNOV AND TANIA M. BARDSLEY <i>Myriotrochus antarcticus</i> sp. nov. (Apodida: Myriotrochidae), a new holothurian species from eastern Antarctica	109
KERRIE M. SWADLING AND IAN A. E. BAYLY Different zooplankton communities in confluent waters: comparisons between three marine bays in Victoria, Australia	113
N. W. ARCHBOLD Nomenclatural note	119

TRANSACTIONS

Obituary—PATRICK SELLAR LANG	i
Obituary—JAMES HAMLYN WILLIS	iii
FIFTY YEARS A GEOLOGIST	xi
J. E. CUMMINS OBE, 1997 Memorial Oration	xiii

PROCEEDINGS
OF THE
ROYAL SOCIETY OF VICTORIA
PEER REVIEWED PAPERS

DIET OF A FAMILY OF POWERFUL OWLS (*Ninox strenua*) FROM WARRANDYTE, VICTORIA

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COOKE, R., WALLIS, R. WEBSTER, A. & WILSON, J. 1997:11:30. Diet of a family of Powerful Owls (*Ninox strenua*) from Warrandyte, Victoria. *Proceedings of the Royal Society of Victoria* 109 (1): 1-6. ISSN 0035-9211.

The diet of a family of powerful owls living at Warrandyte State Park was examined by analysis of 631 regurgitated pellets collected over five years (1991 to 1995). Warrandyte State Park forms a riparian strip along the Yarra River and is 24 km north-east of Melbourne. The Park's habitat has been disturbed in the past and it is surrounded by housing, introduced pastures and orchards. Mammalian prey was found in 98%, birds in 2% and insects in 8% of the pellets. Of the mammals, common ringtail possums occurred most frequently in the pellets, with no seasonal differences in occurrence. In contrast, common brushtail possums (which were found in 29% of pellets with mammalian remains) and sugar gliders (7%) showed seasonal variation in occurrence. The majority of common brushtail possums taken as prey were less than one year old, however, 15% were adults. We conclude that powerful owls feed opportunistically on suitable arboreal marsupials including large common brushtail possums, and that at Warrandyte most prey taken are not dependent on hollows for nesting.

THE POWERFUL owl (*Ninox strenua*) is Australia's largest owl. It occurs on the mainland with most populations concentrated on the eastward side of the Great Dividing Range (Blakers et al. 1984), although breeding pairs have been reported well outside of this range (Rolls 1979; Pavey 1993). Historically, *N. strenua* has been considered a habitat specialist, being most numerous in dense gullies of tall, old-growth forests in hilly or mountainous localities of the coast and the Great Divide (Debus & Chafer 1994).

Powerful owls are considered rare at a national scale (Garnett 1992) and also in Victoria (Department of Conservation and Natural Resources, Victoria 1995). In the Greater Melbourne area the owl is considered threatened (Mansergh et al. 1989). However, there have been recent reports of breeding powerful owls in a wide range of habitats, many of which are disturbed (Debus & Chafer 1994; Pavey 1994). Nevertheless, Chafer (1992) has urged comprehensive studies be carried out on the species' diet and habitat requirements in order to resolve questions of its status and to facilitate its conservation management.

Powerful owls are believed to need large home ranges (about 1000 ha per pair) (Schodde & Mason 1980) in suitable old-growth forest which provide nest hollows for the owls and for their arboreal marsupial prey (Fleay 1968; Seebeck 1976; Roberts 1977). Recent studies, however, have suggested

the species is more flexible in its habitat requirements. For example, Quinn (1993) has reported two breeding pairs of owls less than 400 m apart. In central coastal New South Wales, Chafer (1992) found the species in more locations, in a wider variety of forest types and roost sites and nesting at lower heights than previously recorded. Other studies (e.g. Debus & Chafer 1994; Kavanagh et al. 1995) have found the owls are little affected by habitat modification other than clear-felling and conversion to open landscape. For instance, Kavanagh and Bamkin (1995) have reported *N. strenua* in equal frequencies in unlogged forests and in logged and unlogged mosaics with dispersed coupes. Other reports further suggest that powerful owls can breed and raise young in sites that are affected by human activity, such as urban parks (Pavey 1993, 1995; Chafer 1992), a disturbed forest park (Quinn 1993) and a caravan park (McNabb 1994).

Previous studies have shown that the owls feed mainly on those medium-sized species of arboreal marsupials that are most readily available at a given site, such as common ringtail possums (*Pseudocheirus peregrinus*) (Seebeck 1976; Tilley 1982; Hollands 1991; Chafer 1992; Traill 1993; Lavazanian et al. 1994; McNabb 1996) and greater gliders (*Petauroides volans*) (Fleay 1968; Kavanagh 1988). Pavey (1992), however, disputes the importance of greater gliders in the diet of the

powerful owl which several authors have claimed, for example Tilley (1982) and Kavanagh (1988). There is thus debate in the literature as to whether powerful owls specialise their foraging activities to obtain prey species such as greater gliders in accordance with optimal foraging theory (Kavanagh 1988; Pavey 1992). There is also a question as to whether dietary specialisation on hollow-dependent arboreal marsupials renders the powerful owl vulnerable to habitat disturbance (Debus & Chafer 1994; Lavazanian et al. 1994).

Other possums and gliders, fruit bats, birds and insects are also taken depending on their availability (Tilley 1982; Chafer 1992; Pavey 1994; Pavey et al. 1994; Pavey 1995). The common brushtail possum (*Trichosurus vulpecula*) has been recorded as prey of the powerful owl by numerous authors (e.g. Van Dyck & Gibbons 1980; Debus & Chafer 1994; Lavazanian et al. 1994; Pavey et al. 1994). This species has a major peak in births between March and May and a smaller peak in September and October (Kerle 1984). Common brushtail possum remains in powerful owl pellets have been found by Van Dyck & Gibbons (1980) almost exclusively in spring, suggesting that only juveniles are taken, probably when riding on their mothers' backs. Little evidence is available to indicate that adult common brushtail possums, which weigh up to 4.5 kg (Strahan 1995), are taken as prey by the powerful owl. Adult brushtail possums can weigh more than twice as much as adult powerful owls and thus could be considered a difficult prey item for owls.

In 1990 a breeding pair of powerful owls was located in Warrandyte State Park, an urban, riparian park which is only 24 km from central Melbourne and which fringes the Yarra River. The aims of this study are to describe the seasonal variation in the diet of the owls, and also to determine the ages of common brushtail possums taken as prey.

METHODS

Warrandyte State Park is a 586 ha reserve 24 km north-east of Melbourne. The park is a linear strip of mainly riparian forest dominated by eucalypts (especially *Eucalyptus polyanthemos* and *E. viminalis*) with an understorey of wattles and tall shrubs. The park is positioned at the transition between the suburbs of Melbourne and the more rural setting of the Upper Yarra Valley. There are nearby steeply forested slopes (east of Wonga Park) and forest patches alongside tributaries (e.g. Mullum Mullum Creek) or in small blocks (e.g. Currawong Bush Park) (Department of Conservation and Environment, 1990). However, the

park is mostly surrounded by housing, some pasture and orchards.

The park has been subjected to frequent fuel reduction fires and also wildfires. For instance, since 1857 there have been 11 major wildfires recorded (the most recent of which was in 1969), 16 fuel reduction burns and 11 accidentally started spot fires (Department of Conservation and Environment, 1990).

A total of 631 regurgitated food pellets were collected between 1991 and 1995 from roost sites used by a pair of owls and their young. The owls have been seen in 40 roost trees from seven locations in the Park (Table 1). Six of the locations were adjacent to the Yarra River and the other was 1.5 km from the river.

Pellets were placed in envelopes marked with location and date and sterilised at 100°C for 24 h. Prey items were categorised into major food types and the mammalian prey remains were then separated into skeletal and hair components. A diagnostic aid was developed to help identify mammalian remains. This key contained photographs of bones of the three main mammalian prey species and highlighted the distinguishing characteristics of each species. The principal skeletal parts used were skull (including lower jaw and teeth), humerus, femur, pelvic girdle and scapula. Further details of the diagnostic aid are to be found in Lavazanian (1996) and Cooke (1995). Brunner & Coman (1974) was used to help distinguish between primary guard hairs of the three species.

Skeletal remains of common brushtail possums were categorised into three age classes: juvenile (<1 year old), immature (1–4 years) and adult (>4 years) on the basis of fusion of epiphyses (Kingsmill 1962), shape and size of limb-bones, shape and size of pelvic girdles, skull size, extent of sagittal crest and eruption of teeth (Cooke 1995).

Species	Number
Red box (<i>Eucalyptus polyanthemos</i>)	12
Willow (<i>Salix</i> spp.)	6
Wattles (<i>Acacia</i> spp.)	8
Messmate (<i>E. obliqua</i>)	3
Tea-tree (<i>Leptospermum</i> spp.)	3
Manna gum (<i>E. viminalis</i>)	2
Cherry ballart (<i>Exocarpos cupressiformis</i>)	2
Unidentified eucalypt sapling	1
Hazel pomaderris (<i>Pomaderris aspera</i>)	1
Christmas bush (<i>Prostantha lasianthos</i>)	1
Burgan (<i>Kunzea ericoides</i>)	1

Table 1. Roost trees used by powerful owls at Warrandyte State Park.

RESULTS

More pellets were collected during spring (September–November) than the other seasons. During spring the young owls have emerged from the nest and roost with their parents. The parents are more easy to detect in spring than in other seasons because they remain close to the young. In autumn the juvenile owls fledge and probably leave the parents' home range and the parents often roost separately which makes them more difficult to locate. As well, in winter when the owls roost at times over the river, pellets are not always retrievable. Consequently, fewer pellets were collected in autumn and winter than the other seasons.

Mammals occurred in 98% of the pellets (Table 2). The five pellets without mammals contained bird remains. Insects occurred in 8% of pellets and most frequently during summer and autumn.

The numbers of pellets containing each of the six mammalian prey species identified for each

season is given in Table 3. Common ringtail possums were the most frequent prey item (in 64% of pellets with mammalian remains) although common brushtail possums were also commonly detected (29%). There was no difference across the four seasons in the proportion of pellets containing common ringtail possum (Chi-square test, $P > 0.05$) although there were significant seasonal differences in proportional occurrences of the common brushtail possum ($P < 0.005$) and sugar glider (*Petaurus breviceps*) ($P < 0.05$).

Most of the pellets with brushtail possum remains contained juvenile possums (63%) (Table 4), and most of these were collected during spring. However, 26 pellets (15%) also contained the remains of adult brushtail possums.

DISCUSSION

Other studies we are carrying out suggest there are now likely to be at least five pairs of powerful owls living in an area of 10 000 ha in the Yarra

Food item	Summer	Autumn	Winter	Spring	Total
Mammals	146 (100)	99 (100)	108 (98)	273 (98)	626 (98)
Birds	6 (4)	2 (2)	2 (2)	1 (1)	11 (2)
Insects	34 (23)	15 (15)	1 (1)	3 (2)	53 (8)
Total no. of pellets	146	99	110	276	631

Table 2. Dietary components as the number of pellets in which a prey category was represented of owl pellets collected in each of the four seasons. Values in parentheses are percentages of the number of pellets examined for that season.

Mammalian prey	Summer	Autumn	Winter	Spring	Total
Common ringtail possum (<i>Pseudocheirus peregrinus</i>)	106	75	70	149	400 (64)
Common brushtail possum (<i>Trichosurus vulpecula</i>)	29	14	31	110	184 (29)
Sugar glider (<i>Petaurus breviceps</i>)	12	12	0	21	45 (7)
Yellow-bellied glider (<i>Petaurus australis</i>)	0	0	0	2	2 (0.3)
Rabbit (<i>Oryctolagus cuniculus</i>)	0	0	0	3	3 (0.4)
Cat (<i>Felis catus</i>)	0	0	0	1	1 (0.4)
Unidentifiable	1	0	7	3	11 (1.5)
Total no. pellets	146	99	108	273	626

Table 3. Number of pellets containing mammalian prey for each season. Values in parentheses are percentages of pellets with that species of the 626 pellets known to have mammalian remains.

Age class	Summer	Autumn	Winter	Spring	Total
Adult (>4 years)	4	4	7	11	26 (15)
Immature (1-4 years)	5	3	9	19	36 (22)
Juvenile (<1 year)	16	5	10	73	104 (63)

Table 4. Age classes (remains in 166 pellets) of common brushtail possums taken over the four seasons. Values in parentheses are percentages of possums taken from that age class.

Valley. This habitat is severely fragmented and disturbed by human activities. A recent sighting of a pair of owls which failed to rear young at a site downstream from Warrandyte State Park suggests the owls are expanding in range, certainly into habitats which differ from the dense gullies of tall, old-growth forest in which the species was historically thought to be restricted. These recent sightings support the belief of Debus & Chafer (1994) that the species has wider habitat tolerance than formerly believed and also the findings of Pavey et al. (1994) who studied the owls around Brisbane.

Our data also support dietary studies conducted elsewhere that have found common ringtail possums to be the principal prey species in coastal or lowland sites in Victoria (Seebeck 1976; Tilley 1982; Hollands 1991; Lavazanian et al. 1994). As expected, the diet of the Warrandyte owls is similar to that of a pair of powerful owls at Christmas Hills which is only 15 km north-east of Warrandyte State Park (Lavazanian et al. 1994). Important differences were, however, that fewer birds were found in pellets from the Warrandyte birds (2% occurrence compared with 10% Christmas Hills) and common brushtail possum remains were more frequently detected in pellets of the Warrandyte birds (29% of pellets with mammals compared with 3%). Preliminary spotlighting data suggest that high densities of common ringtail possums live in the Park. Thus Cooke (1995) carried out 17 h of spotlighting over three seasons and 184 possums were observed, of which 162 were ringtail and 22 brushtail possums. However, a survey of local residents indicates brushtail possums are common in properties adjacent to the Park and that many of these possums live in the roofs of homes (Cooke 1995). Another interesting difference concerns the use of hollows and dreys by common ringtail possums.

At Christmas Hills most ringtail possums nest in tree hollows and dreys are rarely seen. As well, sugar gliders and the few common brushtail possums detected in Lavazanian's (1996) spotlighting surveys also occupy tree hollows. In contrast, common ringtail possum dreys are very common in Warrandyte State Park and there appears to be a shortage of tree hollows suitable for nesting possums.

Most common brushtail possums were detected in pellets collected during spring. This is consistent with findings reported elsewhere by Seebeck (1976), Tilley (1982), Van Dyck & Gibbons (1980) and Lavazanian et al. (1994) and is believed to be related to the emergence of young common brushtail possums on to their mothers' backs.

Common brushtail possums are polyoestrous and monovular and give birth to a single young at each parturition (Smith et al. 1969). There is a distinct peak in births between March and May and a lesser peak in September and October (Kerle 1984). The young possums emerge from the pouch four to five months after birth and remain close to their mother, often riding on her back. This can explain the peak in predation of common brushtail possums by the owls in spring and to a lesser extent in autumn. The presence of ten pellets collected during winter with juvenile brushtail possums remains can be explained by collections occurring in early winter. The pellets had been present for some time and were possibly regurgitated during autumn (A. Webster, unpublished data).

Ninety per cent of common brushtail possum remains in pellets could be categorised into age classes (Table 4). The majority (63%) of brushtails taken as prey were less than one year old. Nevertheless, 15% of the remains of brushtail possums taken were classed as older than four years, indicating that powerful owls do indeed take adult common brushtail possums as prey. This observation is noteworthy because of the large size of adult common brushtail possums (adult weight range of possums collected in Melbourne 5.0-3.0 kg; RSPCA, unpublished data). In contrast, Lavazanian et al. (1994) found 50% of common ringtail possums (in which maximum mass is only one quarter that of the brushtail possum) taken by powerful owls at Christmas Hills were adults.

Although it is uncommon for owls to take prey heavier than themselves (Braithwaite 1996), Mooney (1993) reported that masked owls (*Tyto novaehollandiae*) in Tasmania took prey up to two and a half times their own weight, a similar ratio

was observed in our study for powerful owls consuming adult common brushtail possums.

The presence of yellow-bellied gliders (*Petaurus australis*) in two pellets is interesting. Although it has been reported in the diet of powerful owls elsewhere (Debus & Chafer 1994), the yellow-bellied glider is not taken as a major food item even when they are present in the area (Tilley 1982; Kavanagh 1988). Also, yellow-bellied gliders are unknown in Warrandyte State Park, the nearest known location being 17 km away in Kinglake National Park.

Rabbit remains were detected in three pellets. This is unusual as rabbits do not climb trees and powerful owls are believed to mainly take arboreal prey. However, Lavazanian et al. (1994) found rabbit remains in 0.5% of pellets from Christmas Hills, and hares have been reported in powerful owl pellets by Chafer (1992) in New South Wales and by Pavcy (1994) in Queensland. Even more unusual was the occurrence of cat fur in one pellet we found, although Chafer (1992) found two individual cat remains (out of 56 prey items) from pellets collected at Bass Point, south of Wollongong.

Our data suggest powerful owls are opportunistic in that they take those arboreal prey which are easiest to obtain, including adult common brushtail possums which are more common at Warrandyte than at nearby Christmas Hills (Lavazanian et al. 1994). As well, this study casts doubt on the conclusion that the future conservation of the owl is dependent on the continued availability of hollow-dependent marsupial prey; most prey taken nested in dreys (common ringtail possums) or in artificial structures such as house roofs (common brushtail possums).

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REGENERATION OF SOME FOREST AND GULLY COMMUNITIES IN THE ANGAHOOK-LORNE STATE PARK (NORTH-EASTERN OTWAY RANGES) 1-10 YEARS AFTER THE WILDFIRE OF FEBRUARY 1983

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Forest communities in the Angahook-Lorne State Park near Aireys Inlet include dry sclerophyll open-forest dominated by 18 m tall *Eucalyptus tricarpa* and various gully complexes. The number of plant species per community ranges from 43-130 and reflects differences in moisture, soils and topography.

Following the wildfire of February 1983, 77% of all species of vascular plants present before the fire reappeared within the first year and 98% (all but two species) returned within three years. The two species which did not reappear by year 3 (*Amyema pendulum* and *Hymenophyllum cupressiforme*) had still not returned by year 10.

Maximum post-fire species richness of vascular plants occurred in the early years after fire, then decreased by year 10 as vascular plant cover increased. In contrast, maximum post-fire species richness of non-vascular plants occurred 10 years after fire as canopy and understory cover increased. Extensive carpets of two minerotrophic bryophytes (*Marchantia berteroana* and *Funaria hygrometrica*) and the fungus *Gerronema postii* appeared in damper areas of all communities during the first year after fire, and were not seen after year 3.

Approximately 62% of all vascular species which appeared in the first 3 years after fire, and still remained at year 10, had the capacity to regenerate vegetatively (or both vegetatively and from seed). The other 38% of vascular species regenerated from seed only.

The canopy in all communities recovered between 3 and 10 years reaching approximate pre-fire height and cover levels. Rate of recovery was faster in gully complexes than in drier *E. tricarpa* open-forest.

Seventy per cent of all species flowered or produced spores by the end of the third year. Twenty-five per cent of all species of trees and shrubs had not flowered or set seed by year 3, but did so by year 10.

Floristic and structural changes were seen in *E. tricarpa* open-forest where the previously open grassy understorey of *Poa sieberiana* (0.2 m tall) was replaced by a dense (4.0 m tall) understorey of fire induced or 'hard-seeded' shrubs including *Acacia verticillata*, *Goodenia ovata* and *Pultenaea daphnoides*.

Major floristic and structural changes also occurred in a gully complex where a peat fire was ignited by the wildfire and burnt to a depth of over 2 m for 3.5 months after the wildfire. Here the *Eucalyptus obliqua*/*Cyathea australis*/*Prostanthera lasiantha* complex was completely killed and replaced by seedling eucalypts which, by 10 years post-fire, formed a dense canopy (18 m tall) with no discernible understorey.

ON 17 February 1983 (Ash Wednesday) a wildfire burnt approximately 40 000 hectares of vegetation near Anglesea and Aireys Inlet, in the north-eastern Otway Ranges, Victoria (Rawson et al. 1983). Prior to 1983 there had been no published study on the fire ecology of the flora of this area. Following the wildfires, a ten year study of the post-fire recovery of vegetation and fauna was initiated (Reilly 1985, 1991a, 1991b; Wilson & Moloney 1985a, 1985b; Andersen 1987; Wark et al. 1987; Wark 1996).

The aims of the botanical study were to describe vegetation regeneration following wildfire in six of the major plant communities in the district (coastal heath, heath woodland, open-forest, sand-dune scrub, swamp thicket and gully complexes), and to provide information for use in the planning of conservation management. Regeneration of the heath and heath woodland communities in the first 10 years after fire has already been described (Wark et al. 1987; Wark 1996).

This paper presents data on regeneration of

Site	Location Height above SL Topography Geological origin	Fire history before Ash Wed. (Feb. 1983)	Fire intensity Ash Wed. (Feb. 1983)	Subsite	Aspect	Soil type (A Horizon) 3 years after fire	Vegetation formation	Dominant species	Approx.** prefire height (m)	Height 3 years after fire (m)	No. of quadrats Yr 1, Yr 3	Area sampled (ha)
E (Bambra Road, Angahook -Lorne State Park)	2 km inland, 50-150 m above SL in watershed of Painkalae Creek. Topography hilly. Soils derived from Tertiary Eastern View Formation	Control burn approx. 1940. Bushfire 1962.	All Crown fired	E1	N/NE 11°	27 cm sandy clay loam, over sandy clay	Open Forest	<i>Eucalyptus tricarpa*</i>	18.2	14.6	12, 12	2.0
				E2	S/SW 12°	32 cm sandy loam	Open Forest	<i>Eucalyptus tricarpa</i> , <i>Eucalyptus cypellocarpa</i> <i>Eucalyptus aromaphloia</i> and others	17.2	13.9	15, 15	2.0
				E3	N/NE 11° (bottom of gully leading to Ironbark Gorge)	ND *	Gully Complex	<i>Eucalyptus cypellocarpa</i> <i>Pomaderris aspera</i>	36.0	32.0	3, 3	0.1
F (near Distillery Creek Road, Angahook -Lorne State Park)	4 km inland, 50 m above SL in watershed of Distillery Creek. Topography hilly. Communities sampled were at bottom of gully. Soils derived from Tertiary Eastern View Formation	No fire for approx. 100 years	Crown fired	F1	N 0° (bottom of gully beside Distillery Creek)	>90 cm peaty loam	Gully Complex	<i>Eucalyptus obliqua</i> <i>Cyathea australis</i> <i>Prostanthera lasianthus</i>	14.0	14.0	5, 5	0.1
				F2	N 0° (bottom of gully)	>90 cm burnt peat	Modified Gully Complex	<i>Eucalyptus obliqua</i> <i>Eucalyptus willisii</i>	14.0	5.0	2, 5	0.1

Table 1. Site descriptions of forest and gully communities. *Modified by human interference. **Tallest stratum. *ND=not done.

E. tricarpa open-forest and various gully complexes ten years after the 1983 fire and describes their floristics and structure. Regeneration strategies and post-fire flowering response of species are also described. Mammal, bird and insect data have been studied and reported separately (Reilly 1985, 1991a, 1991b; Wilson & Moloney 1985a, 1985b; Andersen 1987).

SITE DESCRIPTIONS

Two sites (E and F) which supported native vegetation, and which were relatively undisturbed by European man (Fig. 1, Table 1), were selected in undulating terrain on soils derived from Tertiary sediments known as the Eastern View Formation (Pitt 1977, 1981). The sites were located 2.5–4.0 km inland from the coast, in the Angahook-Lorne State Park, near Aireys Inlet. Each contained one or more plant communities (subsites), including *Eucalyptus tricarpa* (red ironbark) open-forest (subsite E1), *E. tricarpa* mixed open-forest (subsite E2), and various gully complexes (subsites E3, F1 and F2). The term open-forest follows Specht (1970), the term 'gully complex' is used because these small riparian communities were very narrow, disjunct and uncommon, and contained varied proportions of broad leaf and sclerophyll vegetation.

Subsite E1 was on a north-facing slope. Here the overstorey was an almost pure stand of *E. tricarpa*, generally of a similar age and density. On the adjacent southerly slope (subsite E2) the overstorey eucalypts were of mixed age, density and species and included *E. tricarpa*, *Eucalyptus cypellocarpa*, *Eucalyptus aromaphloia* and others. Both subsites E1 and E2 had light grassy understoreys before the fire (Parsons et al. 1977).

Both sites had been affected by timber cutting between 1860 and 1920, and were controlled by the Forests Commission of Victoria between 1921 and 1987. During this second period, understorey reduction and thinning was carried out from time to time, as part of local fire-prevention strategies (P. Denham, pers. comm.). It is not known whether subsites E1 and E2 were affected by these practices.

The gully complexes studied were discontinuous, often occurring in narrow bands (max. width 20–50 m) beside semi-permanent streams. All were surrounded by dry sclerophyll open-forest with a eucalypt overstorey. The complex adjacent to the creek running through Ironbark Gorge (subsite E3) occurred on silty soil, and those adjacent to Distillery Creek (subsites F1 and F2) on peaty soil and (after Feb. 1983) burnt peat soil

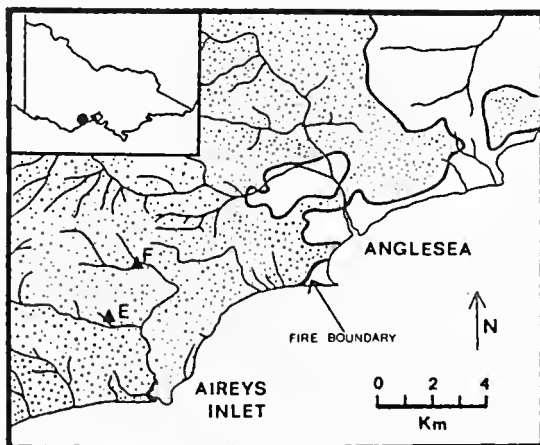


Fig. 1. Locality map showing location of the eastern Otway Ranges, Victoria and sites E and F near Anglesea. Stippling indicates the area burnt on 17 February 1983. The fire advanced from the south west.

respectively. Overstorey species in these included *Eucalyptus cypellocarpa* and *Eucalyptus obliqua*, varying proportions of the broad-leaved understorey shrubs *Pomaderris aspera* and *Prostanthera lasiantha* and the ferns *Cyathea australis* and *Todea barbara*.

The previous fire history of each site differed (Table 1). The high-intensity wildfire of February 1983 destroyed all ground strata vegetation and crown-fired the eucalypt overstorey at all subsites (Table 1). The fire occurred following a drought in 1982, which intensified in January, February and March 1983 (in 1982 the total annual rainfall of Anglesea was 452 mm compared with the annual mean of 657 mm). Over 80 mm of rain fell one month after the fire and then at 3, 7 and 8 months post-fire causing soil erosion and hill wash at subsites E1, E2 and E3, and often removing the top 2–4 cm of humus and ash-rich soil of the upper A horizon. Total rainfalls for 1983–1993 were about or above average except for years 1986, 1988, 1990 and 1991, when they were 622, 643, 596 and 614 mm respectively (Wark et al. 1987; Wark 1996).

A peat fire, started by the wildfire, established at subsite F2 and gradually burnt the soil in half the gully to a depth of about 2.0 m. It was finally extinguished by early winter rains in June 1983. In the area where this peat fire burnt for 3 months, the ground sank, the creek bank collapsed, and large areas of burnt peat were washed away.

Because of the extent of the Ash Wednesday fires, no unburnt sites comparable with sites E and F were available for study.

METHODS

Soils

Soil profile data. Methods of soil description and analysis follow Wark et al. (1987). Surface (0–10 cm) soil samples collected at 2 months and 1 and 2 years after fire were analysed for pH, available P, total Kjeldahl N, organic C, and exchangeable Na, K, Ca and Mg by the State Chemistry Laboratory, Victoria. The A horizon profile was examined at 3 years (by Dr D J Robertson, Wark et al. 1987) by digging pits down to the upper B2 horizon, and recording colour, texture and depth.

Pot experiments. A bioassay was carried out to assess fertility of black unburnt peat soil from F1 and red burnt soil from F2 using samples collected two years after the wildfire. Seed of *Eucalyptus obliqua* was collected adjacent to subsites F1 and F2. *E. obliqua* seedlings were grown at Aireys Inlet for 8 months on the two soils (1 seedling/75 mm diameter pot, 15 pots/treatment) in a shade house from autumn to spring. Shoot height of each group was measured monthly for 8 months, and mean growth rates determined. After 8 months, dry weight of roots and shoots and root/shoot ratios were determined.

Vegetation

Pre-fire data. Detailed species lists of vascular plants existed for each site prior to the 1983 fire (White 1982). However, no quantitative data on pre-fire floristics or vegetation structure were available. Approximate pre-fire height was interpreted from pre-fire photographs and the height of burnt tips. Approximate pre-fire projective cover was also estimated from pre-fire field observations and photographs.

Data collection. Forty 1×3 m permanent quadrats (Table 1) surrounded by permanent extended plots (11×13 m) were used for data collection at 2, 6 and 10 months and in spring 1, 3, 7 and 10 years after fire. At site E, quadrats were in groups of three 20 m apart set at 90 m intervals along transect lines 300–350 m long. At subsite F1, quadrats were placed in a Maltese cross, and at subsite F2 they were distributed randomly.

Methods used to collect and analyse floristic and structural data (including canopy regrowth)

and determine flowering and regeneration response have been previously described (Wark et al. 1987; Wark 1996).

Total species lists were made for each subsite at each survey, and these used to supplement quadrat data on floristics, flowering and regeneration strategies. As in Wark et al. 1987 and Wark 1996, the term 'total number of species' at a site (or subsite) refers to the total number of species recorded in the quadrats plus any additional species recorded at the site (or subsite). In the present paper, quadrat data alone are used to analyse the relationship between plant species richness and total vascular plant cover.

Girth of trunks of the overstorey and understorey were measured at 1.45 m (girth at breast height, GBH). Data on the eucalypt overstorey in open-forest was derived from measurements of a minimum of 20 trees of the tallest stratum. In this paper, the term understorey (or shrub stratum) will include the ground stratum; the term herb will be used to mean an herbaceous species; and the term graminoid will not be used.

Nomenclature of vascular plants follows Ross (1996); for Orchidaceae—Backhouse & Jeanes (1995); mosses—Scott & Stone (1976); liverworts—Scott (1985); and lichens—Filson & Rogers (1976). Introduced species were identified by the National Herbarium of Victoria.

The species described as *Marchantia polymorpha* in Wark et al. 1987 was incorrectly identified. It was in fact *Marchantia berteroana* Lehm. & Lindenb. (Scott 1985). Similarly, the fungus *Omphalia chromacea* is now known to be *Gerronema postii* (Fr.) Singer (May & Fuhrer 1989); and the herb *Viola hederacea* ssp. *sieberiana* now known to be *Viola cleistogamoides*. Name changes of vascular plants which have occurred since the first paper in this series (Wark et al. 1987) are given in Wark 1996 and in the Appendix of the present paper.

Regeneration strategies terminology follows Purdie (1977a, 1977b), namely: OSR=obligate seed regenerator (regenerating from seed or propagules only); FRR=facultative regrowth regenerator (regenerating by regrowth, and from seed or propagules); ORR=obligate regrowth regenerator (regenerating by regrowth only).

RESULTS

Soils

Profiles. Soil profile data are given in Table 2. At E1 and E2, hill wash and soil erosion occurred one month after the fire, and in places the top

Community (subsite)	Year after fire	pH (H ₂ O)	Exch. Na c mol(+)/kg	Exch. K c mol(+)/kg	Exch. Ca c mol(+)/kg	Exch. Mg c mol(+)/kg	Avail. P mg/kg	Total Kjeldahl N g/g ⁻²	Organic C g/g ⁻²	C/N
Open forest (E1)	1*	5.8	0.50	0.28	0.98	2.09	2.0	0.11	3.2	25.0
	2**	5.7	0.45	0.23	0.80	1.34	1.3	0.13	3.3	31.0
Open forest (E2)	1	5.3	0.22	0.23	0.48	0.48	1.6	0.10	2.2	24.0
	2	5.5	0.33	0.23	0.77	0.58	1.4	0.11	2.7	15.0
Gully complex (F1)	1	5.1	0.30	0.60	0.10	1.60	3.5	0.49	9.3	19.0
	2	5.5	0.57	1.10	0.60	4.18	1.7	0.60	12.1	20.0
Modified gully complex (F2) (burnt peat)	1	5.5	0.20	0.60	1.30	1.28	11.4	0.30	2.1	7.0
	2	6.0	<0.09	0.80	0.50	1.28	3.6	0.21	3.2	15.0

Table 2. Soil analysis of the A horizon (0–10 cm) of forest communities 1 and 2 years after fire. *Year 1 values are from single samples. **Year 2 values are from composite samples of 40 cores.

0–6 cm of the humus-rich and ash-rich A1 horizon was removed exposing a compacted A2 horizon of 6–32 cm. Cracking of this layer was common and patches of hydrophobic soil were observed.

The soil at subsite F1 was a black peaty loam >0.9 m in depth. Burning of this peaty loam (subsite F2) produced a friable material 0.9 m–2.0 m deep. In this paper, this material will be called 'burnt peat'. The colour of this burnt peat was in the Munsell 'red' Range. During the 3 years following the fire, a brown 5 cm litter layer developed on the top of the burnt peat. The burnt peat gradually sank 0.5–1.0 m in the years following the fire and erosion channels up to 1.5 m deep developed near the creek.

Chemical analyses. Topsoil samples taken at the subsites 1 and 2 years post-fire ranged in pH from 5.1–6.0 (Table 2). Subsites E1 and E2 were both low in nutrient cations and organic matter. The soil at subsite F1 was higher in organic matter and N than subsite F2. The soil at subsite F2 was high in available P, 1 year after the fire. Soils of both subsite F1 and F2 retained high levels of exchangeable K between years 1 and 2.

Analyses of 1 and 2 year post-fire topsoil samples showed no significant change in nutrient levels between these times (Table 2, $P > 0.05$, *t* test), and suggests that any 'ash bed' effect had disappeared by the first year. Unfortunately topsoil samples collected two months after the fire were mislaid.

Pot growth experiments with *E. obliqua*. Growth of *E. obliqua* was faster on peat soil derived from subsite F1 ($P > 0.05$, *t* test) than from F2. Seedlings on the burnt peat grew rapidly initially then slowed in growth and became chlorotic. Seedlings planted on unburnt peat grew steadily and appeared normal compared with those on burnt peat. Mean root/shoot ratios at the end of the experiment were 0.39 and 0.61 (for subsites F1 and F2 respectively).

Throughout the experiment, levels of available P remained high in burnt (cf. unburnt) soil.

Vegetation

Floristics. The floristics of the plant subcommunities one, three and ten years post-fire are presented as presence-absence data in Table 3.

(a) **Number of species.** A total of 182 species of vascular plants was recorded prior to the fire (Table 3). With the exception of 2 species, all reappeared in the first 3 years after fire. The

mistletoe *Anyema pendulum* and the filmy-fern *Hymenophyllum cupressiforme* (which were present before the fire) did not reappear in the 10 years following the fire. A total of 44 species of non-vascular plants (liverworts, mosses and lichens) appeared sequentially during the 10 years after fire.

A total of 9 tree species, 40 shrubs, 116 species of herbs (including 20 orchid species), 7 creepers and climbers, 8 ferns and 44 species of non-vascular plants were present post-fire (Table 3).

(b) **Diversity of plant communities.** Plant communities were floristically diverse (Table 3). Species numbers 10 years post-fire ranged from 120–130 for open-forest subcommunities, 76–82 for gully complexes, and 43 for the modified gully complex. Forty to seventy per cent of species in each sub-community were sampled in the 1×3 m permanent quadrats at year 3, giving a species richness in quadrats of 22–48 species. Nine species were found in all 5 subcommunities, including *Acacia verticillata*, *E. cypellocarpa*, *Goodenia ovata*, *Tetrarrhena juncea*, *Gahnia radula* and several species of herbs and nonvascular plants. Floristics of these subcommunities are presented as presence-absence data in Table 3.

Computer analysis of combined year 1 and year 3 data (by Dr D. J. Robertson, Charles Sturt University; see Wark et al. 1987), using both classification and ordination techniques (data not presented here), confirmed the presence of at least 5 distinct subcommunities (all with shrubby understoreys—subsites E1, E2, E3, F1 and F2, Table 3) and identified floristic differences between them. Ordination results confirmed the classification data.

Floristic differences and stature of dominants between open-forest and gully complexes appeared to reflect variations in drainage, soils and topography. Open-forest occurred on sloping sites with sheet-eroded silty-clay soils, whereas gully complexes occurred beside creeks, on silty or peaty soils.

(c) **Changes in species richness with time.** Maximum post-fire species richness occurred in the early years after fire (Table 3, Fig. 2).

In both forest and gully communities, the species richness of vascular plants in quadrats decreased (Figs 2A, 2C) as vascular plant cover increased (Figs 2B, 2D). In contrast, in forest and gully communities the species richness of non-vascular plants either increased or increased then plateaued (Figs 2A, 2C) as vascular plant cover increased (Figs 2B, 2D).

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Trees **					
Myrtaceae					
<i>Eucalyptus aromaphloia</i>		(1) (3) (10)			
<i>Eucalyptus baxteri</i>				1 3 10	(3)
<i>Eucalyptus cypellocarpa</i>	1 3 10	1 3 10	1 3 10	1 3	1 (3)
<i>Eucalyptus globulus</i> ssp. <i>bicostata</i>		(1) (3) (10)			
<i>Eucalyptus obliqua</i>		1 3 10		1 3 10	1 3 10
<i>Eucalyptus ovata</i>					1
<i>Eucalyptus tricarpa</i>	1 3 10	1 3 10	(1) (3) (10)		
<i>Eucalyptus viminalis</i>				(1) (3)	
<i>Eucalyptus willisii</i>	(1) (3) (10)	1 (3)		1 3	1 3 10
<i>Eucalyptus</i> (spp.)	1 10	1 3 10	1	1	1
Tall shrubs †					
Labiatae					
<i>Prostanthera lasianthos</i>			1 3 10	1 3 10	(10)
Mimosaceae					
<i>Acacia dealbata</i>	(1) (3)		(10)		
<i>Acacia mearnsii</i>	(1) (3) (10)				
<i>Acacia melanoxylon</i>	(1) (3) (10)				
<i>Acacia pycnantha</i>	(1) (3) (10)	(1) (3) (10)			
<i>Acacia</i> spp.			(10)		
Santalaceae					
<i>Exocarpos cupressiformis</i>	1 (3)	(1) 3			
Shrubs †					
Asteraceae					
<i>Olearia argophylla</i>			(1) (3) (10)		
<i>Olearia lirata</i>				(3) (10)	
<i>Olearia phlogopappa</i>	1 3 10	(1) (3) (10)	1 3 10	(1) (3) (10)	
<i>Olearia ramulosa</i>	(1) (3)				
<i>Olearia teretifolia</i>	(1) 3 (10)				
<i>Ozothamnus ferrugineus</i>		(10)	(10)	(3) (10)	
Dilleniaceae					
<i>Hibbertia riparia</i>		(1) (3) (10)			
Epacridaceae					
<i>Acrotriche serrulata</i>		(1) 3 10			
<i>Astroloma humifusum</i>	(1) (3) (10)	(1) (3) (10)			
<i>Epacris impressa</i>	(1) 3 10	1 3 10	1 3 10		
<i>Lissanthe strigosa</i>	(1) (3)				
Goodeniaceae					
<i>Goodenia ovata</i>	1 3 10	1 3 10	1 3 10	1 3 (10)	1 3
Fabaceae					
<i>Indigofera australis</i>			(1) (3) 10		
<i>Pultenaea daphnoides</i>	1 3 10	1 3 10		1 (3)	
<i>Pultenaea scabra</i>	(1) (3) (10)				
Loranthaceae					
<i>Amyema pendulum</i> †					
Mimosaceae					
<i>Acacia acinacea</i>	(1) (3)				
<i>Acacia genistifolia</i>	(1) (3) (10)	(1) (3)			
<i>Acacia mucronata</i>	(1) (3) (10)				
<i>Acacia myrtifolia</i>	(1) (3) (10)	(1) (3)			

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
<i>Acacia verniciflua</i>	1 3 10	1 3 10	(1) (3) (10)		
<i>Acacia verticillata</i>	1 3 10	1 3 10	1 3 10	1 3 10	1 3 10
<i>Acacia</i> spp.	(1)	(1)	(1) (10)	1	
Myrtaceae					
<i>Leptospermum</i>					
<i>continentale</i>			(10)	1 (3) (10)	(3)
<i>Melaleuca squarrosa</i>				(1) (3) (10)	
Pittosporaceae					
<i>Bursaria spinosa</i>		(1) (3) (10)	(10)		
Proteaceae					
<i>Lomatia ilicifolia</i>		(1) (3) (10)			
Rhamnaceae					
<i>Pomaderris aspera</i>			1 3 10	3 (10)	
<i>Pomaderris ferruginea</i>	(1) 3 10			(3) (10)	
<i>Pomaderris elachophylla</i>				3 (10)	(3)(10)
<i>Spyridium parvifolium</i>	(10)	1 10	1 3 10	1 3 10	10
Rubiaceae					
<i>Coprosma quadrifida</i>			(1) (3) (10)		
Rutaceae					
<i>Correa reflexa</i>			(1) 3 10		
Solanaceae					
<i>Solanum laciniatum</i>	(1) (3)				
Thymelaeaceae					
<i>Pimelea humilis</i>	(1) (3) (10)	(1) (3)			
<i>Pimelea linifolia</i>	(3)				
Lichens [†]					
<i>Cladia aggregata</i>	(3) 10	10		10	
<i>Cladonia cervicornis</i>					
ssp. <i>verticillata</i>	10				
<i>Cladonia chlorophaea</i>	10				
" <i>corniculata</i>	10				
" <i>ramulosa</i>	10				
" <i>scabriuscula</i>	10				
" <i>tessellata</i>	10				
" spp.	10	10			(10)
<i>Psoroma</i> sp.					10
<i>Thyanothecium scutellatum</i>	10	10			
<i>Usnea</i> sp.? <i>confusa</i>	10				
" ? <i>inermis</i>	10				
Unidentified spp.	1 (3)	1		(3)	(3)
Liverworts [†]					
<i>Asterella drummondii</i>			(3)	3	3
<i>Anthoceros laevis</i>			3	3	
<i>Cephaloziella exilisflora</i>		10		3 10	3
<i>Lethocolea pansa</i>		3	3		
<i>Lophocolea semiteres</i>		10		3 10	3 10
<i>Marchantia polymorpha</i>	1	1	1 3	1 3	1 3
<i>Symphogyna podophylla</i>				3	
Unidentified spp.				3	3
<i>Chaetophyllopsis</i>					
<i>whiteleggei</i>		(10)			

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
<i>Lepidozia laevifolia</i>		10			
<i>Lophocolea muricata</i>					10
<i>Metzgeria decipiens</i>				10	
<i>Riccardia aequicellularis</i>	10	10	10		
Fungi †					
<i>Gerronema postii</i>	(1)	(1)	(1)	(1) 3	
Unidentified spp.	(3) (10)	(3) (10)	(3) (10)	(1) (3) (10)	(1) (3) (10)
Mosses †					
<i>Barbula calycina</i>	3 10	3 10	3		
<i>Breutelia affinis</i>	10			3	
<i>Bryum billardieri</i>		3		3 10	3 10
<i>Bryum campylothecium</i>	10	10			
<i>Bryum capillare</i>	(10)				
<i>Bryum pachytheca</i>	3	3			
<i>Bryum</i> sp.		10			
<i>Campylopus australis</i>	(10)	10			
<i>Campylopus introflexus</i>	3 10	3 10	3	3 10	(10)
<i>Campylopus pyriformis</i>		10		3	
<i>Campylopus</i> sp. nova		10			10
<i>Ceratodon purpureus</i>	3	3	3	3	3
<i>Fissidens tenellus</i>		10			
<i>Funaria hygrometrica</i>	1 3	1 3	1 3	1 3	1 3
<i>Hypnum cupressiforme</i>				10	
<i>Polytrichum juniperinum</i>	3 10	3	3	3	3 10
<i>Ptychomnion aciculare</i>		10		10	10
<i>Senecioiophyllum amoenum</i>		10	(10)	10	10
<i>Tayloria octoblepharis</i>		10			
<i>Wijkia extenuata</i>		10			10
Unidentified spp.	1 3	1 3	1 3		
Ferns & Allies †					
<i>Adiantum aethiopicum</i>			(1) (3) (10)		
<i>Blechnum cartilagineum</i>			1 3 (10)		
<i>Blechnum nudum</i>				1 3 10	
<i>Cyathea australis</i>			(1) (3) (10)	1 3 10	10
<i>Gleichenia microphylla</i>				(3) (10)	
<i>Hymenophyllum</i>					
<i>cupressiforme</i> ††					
<i>Hypolepis rugosula</i>			(3) (10)		3 (10)
<i>Pteridium esculentum</i>		1 3 10	1 3 10	1 3 10	1 3 10
<i>Todea barbara</i>				1 3 10	
Unidentified (young) spp.				3 (10)	
Sedges & Rushes †					
Cyperaceae					
<i>Gahnia radula</i>	1 3 10	1 3		10	
<i>Gahnia sieberiana</i>			(1) (3) (10)	1 3 10	(3)
* <i>Isolepis hystrix</i>				1	
<i>Isolepis inundata</i>				1	
* <i>Isolepis marginata</i>	1	1	1	1 3	
<i>Lepidosperma elatius</i>			(10)	1 3 10	1 3 (10)
<i>Schoenus apogon</i>			3	1	

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Juncaceae					
<i>Juncus pauciflorus</i>				3	3
<i>Juncus planifolius</i>				1	
<i>Luzula meridionalis</i>			3		
Grasses [†]					
Gramineae					
<i>Agrostis avenacea</i>		1			
* <i>Aira caryophyllaea</i>	3	1 3	3		
* <i>Anthoxanthum odoratum</i>		1			
<i>Austrostipa semibarbata</i>	(1) (3)				
<i>Austrostipa rudis</i>	(1)				
* <i>Briza minor</i>			(3)		
<i>Danthonia geniculata</i>	(1)				
<i>Danthonia induta</i>	1	(1)			
<i>Danthonia pilosa</i>	(1)				
<i>Danthonia procera</i>	(1)				
<i>Danthonia setacea</i>	(1)				
<i>Danthonia</i> spp.		(10)			
<i>Deyeuxia densa</i>		3	3	1	
<i>Deyeuxia quadriseta</i>		1	1		
<i>Dichelachne rara</i>	1 3	1 3	3		
<i>Echinopogon ovatus</i>	(1)				
* <i>Holcus lanatus</i>	(1)				
<i>Joycea pallida</i>		(1)			
<i>Microlaena stipoides</i>	1	1	1		
<i>Notodanthonia</i> <i>semianularis</i>	(1)				
<i>Poa morrisii</i>		10 (1)			
<i>Poa sieberiana</i>	1 3 10	1 3 10	1 3		
<i>Poa tenera</i>				(10) 1 3	10
<i>Tetrarrhena distichophylla</i>	1 3 10				
<i>Tetrarrhena juncea</i>	3 10	1 3 10	1 3 10	1 3 10	1 3 10
* <i>Vulpia myuros</i>	(1) (3)				
Unidentified grasses	1 3 10	3 10	3 (10)	1	
Orchids [†]					
Orchidaceae					
<i>Acianthus caudatus</i>	(3)				
<i>Acianthus pusillus</i>	1 (3) 10				
<i>Caladenia cardiochila</i>	(1) (10)			(10)	
" <i>catenata</i>	(3) (10)	(1) (3)			
" <i>tentaculata</i>	(3) (10)	(1)			
" <i>menziesii</i>	1	1 3			
" <i>reticulata</i>		(1) (3)			
<i>Cyrtostylis reniformis</i>		3			
<i>Dipodium punctatum</i>	(1) (3)	(1)			
<i>Eriochilus cucullatus</i>	(1) (3)				
<i>Prasophyllum odoratum</i>	10	1 (3)			
<i>Pterostylis longifolia</i>	(3) 10	(3) 10			
<i>Pterostylis nutans</i>	10		(1)		
<i>Pterostylis nana</i>	(3) 10		3		
<i>Pterostylis parviflora</i>		3			
<i>Pterostylis sanguinea</i>		(1)			

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
<i>Thelymitra flexuosa</i>	3				
<i>Thelymitra ixioides</i>	(3) 10				
<i>Thelymitra pauciflora</i>	(3) (10)				
<i>Thelymitra rubra</i>	(3)				
<i>Thelymitra</i> spp.	(1) (3)				
Lilies & Irises [†]					
Liliaceae					
<i>Caesia parviflorus</i>		(1) (3)			
<i>Burchardia umbellata</i>	3 10	1			
<i>Dianella revoluta</i>	(10)	1			
<i>Lomandra filiformis</i>	1 3 10	1 3 10			
" <i>longifolia</i>	10	1 3 (10)		3	
" <i>multiflora</i>		(1) (3)			
" <i>micrantha</i>		(1) (3) (10)			
<i>Lomandra</i> spp.	(1) 10	(1) 10			
<i>Thysanotus juncifolius</i>				1	
" <i>tuberosus</i>		1 3			
" <i>patersonii</i>	1 3 10				
Herbs [†]					
Asteraceae					
* <i>Aster subulatus</i>			3	3	3 10
* <i>Carduus tenuiflorus</i>				1	
* <i>Cirsium vulgare</i>	(1) 3			1 (3)	
<i>Euchiton involucrat</i>		1 3 (10)	(1) (3)		
<i>Euchiton sphaericus</i>			(1)		
<i>Ozothamnus ferrugineus</i>				(3)	(3)
<i>Helichrysum leucopsidenm</i>		(1)			
<i>Helichrysum scorpioides</i>	(1)				
* <i>Hypochoeris radicata</i>	(1) (3) (10)				
<i>Lagenifera gracilis</i>	1 3 (10)				
<i>Lagenifera stipitata</i>	(1)				
<i>Leptorhynchus linearis</i>	(1)				
<i>Leptorhynchus squamatus</i>	(1)				
<i>Senecio velleioides</i>			(1) 3	1	
<i>Senecio</i> spp.					3
* <i>Sonchus oleraceus</i>			3		
Boraginaceae					
<i>Cynoglossum suaveolens</i>	(1) (3)	(1) (3)			
Brunoniaceae					
<i>Brunonia australis</i>		1 3			
Campanulaceae					
<i>Wahlenbergia gracilentia</i>	(1) (3)	1 3	3	1	
<i>Wahlenbergia stricta</i>	(1) (3) (10)	(10)			
Caryophyllaceae					
<i>Stellaria flaccida</i>			1 3 10	1 3 10	1 3 10
<i>Stellaria pungens</i>		1 (10)			
* <i>Stellaria media</i>		1			
Cruciferae					
<i>Rorippa dictyosperma</i>			1	1	
Droseraceae					
<i>Drosera peltata</i>					
spp. <i>auriculata</i>	1 3 (10)	1 3 10			

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
<i>Drosera peltata</i>	1 3 (10)	1 3 10	(1) 3	3	
<i>Drosera macrantha</i>		(1) 10			
<i>Drosera whittakeri</i>		(1) (3)			
Euphorbiaceae					
<i>Poranthera microphylla</i>	(1)	(1)			
<i>Phyllanthus gunnii</i>				3	
Gentianaceae					
* <i>Centaurium spicatum</i>	(1) (3) (10)			(10)	
Geraniaceae					
<i>Geranium solanderi</i>	1 3 (10)	1 3	1 3 10		
<i>Pelargonium australe</i>	1	1	1		
<i>Geranium</i> spp.		(1)	(1)		
Goodeniaceae					
<i>Goodenia lanata</i>	1 (3)	1 3 (10)			
Haloragaceae					
<i>Gonocarpus tetragynus</i>	1 3	1 10	1 3	1 3	1 3
Hypericaceae					
<i>Hypericum gramineum</i>	1 3 (10)				
Lobeliaceae					
<i>Lobelia gibbosa</i>	(1)	(1)			
<i>Lobelia rhombifolia</i>	(1)				
Oxalidaceae					
* <i>Oxalis corniculata</i>	1 3 10		1 3 10	1 3 (10)	
Plantaginaceae					
<i>Plantago varia</i>	1 3	1 3 10	3		
Rosaceae					
<i>Acaena novae-zelandiae</i>		(1) (3)			
Rubiaceae					
<i>Asperula scoparia</i>	10		1	1 3 10	
<i>Galium binifolium</i>	1 3 (10)		(10)		
<i>Opercularia varia</i>	1 3 (10)	1 3	1 3	1	1
Scrophulariaceae					
<i>Veronica calycina</i>			1 3		
<i>Veronica derwentiana</i>			(1) 10		
Violaceae					
<i>Viola hederacea</i>	(1) 3 (10)	1 3 10	1 3 10	1 3 10	
<i>Viola cleistogamoides</i>				(1) 3 10	1 3
Convolvulaceae					
<i>Dichondra repens</i>	10	(3)			
Umbelliferae					
<i>Hydrocotyle callicarpa</i>	1	1	1 (10)		
<i>Hydrocotyle hirta</i>			1	1 3 10	
<i>Hydrocotyle laxiflora</i>	1	1			
Creepers & Climbers †					
Lauraceae					
<i>Cassytha glabella</i>	1 (3)	1 (3) (10)		1	1
<i>Cassytha melantha</i>	3	3			
Pittosporaceae					
<i>Billardiera scandens</i>	(1) 3 (10)	(1) 3 10	1 3 10	1 3 10	
Polygalaceae					
<i>Comesperma volubile</i>	3 (10)	(1) 3 10		(3)	
Ranunculaceae					
<i>Clematis aristata</i>		1 3 10	1		

Table 3 continued next page (see legend on page 19)

Subsite Vegetation formation	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Fabaceae <i>Kennedia prostrata</i> <i>Glycine clandestina</i>	1 3	1 3	1 3		
Seedlings					
Monocotyledon	1	1	1	1	1
Dicotyledon	1 10	1	1	1	1
Sub-total vascular species in quadrats Year 1, Year 3, Year 10	35, 34, 28	46, 36, 25	30, 33, 25	39, 34, 24	14, 14, 9
Sub-total additional vascular species at site Year 1, Year 3, Year 10	48, 39, 30	35, 26, 17	15, 12, 16	4, 10, 11	-, 6, 4
Total vascular species ^δ Year 1, Year 3, Year 10	83, 73, 58	81, 62, 42	45, 45, 41	43, 44, 35	14, 20, 13
Sub-total non-vascular species in quadrats Year 1, Year 3, Year 10	3, 6, 17	3, 8, 19	2, 8, 1	2, 14, 10	2, 8, 10
Sub-total additional non- vascular species at site Year 1, Year 3, Year 10	1, 2, 2	1, 2, 1	1, 1, 1	1, 3, -	2, 2, 1
Total non-vascular species ^δ Year 1, Year 3, Year 10	4, 8, 19	4, 10, 20	3, 9, 2	3, 17, 10	4, 10, 11
Total species ^δ Year 1, Year 3, Year 10	87, 81, 77	85, 72, 62	48, 34, 43	46, 61, 45	18, 30, 24
Total species ^δ Years 1-3 combined	106	100	62	74	32
Total species ^δ Years 1-10 combined	130	120	76	82	43
Total species ^δ Years 1-10 combined	224 species 180 species vascular plants 44 species non-vascular plants				

Table 3. Floristic comparisons between subsites 1, 3 and 10 years after fire. Key: 1=present in quadrats year 1; 3=present in quadrats year 3; 10=present in quadrats year 10; (1)=present at site year 1; (3)=present at site year 3; (10)=present at site year 10; *introduced species; **12×13 m quadrats; †1×3 m quadrats; ^δ=total species present in quadrats plus additional species present at site. ^v*Amyema pendulum*—present at subsites E1 and E2 before the fire in the eucalypt canopy at 15–20 m. Not recorded years 1–10 post-fire. ^w*Hymenophyllum cupressiforme*—present before the fire at subsite F1, growing on *Cyathea australis*. Not recorded years 1–10 post-fire.

Combining site and quadrat data, maximum post-fire species richness of vascular plants occurred during years 1–3, decreasing by year 10 to 54% of the years 1–3 level (180 species years 1–3 combined; 97 species year 10; Table 3). However, the species richness of non-vascular plants in

years 1–3 combined was 50% that observed in year 10 (18 species years 1–3 combined; 35 species year 10; Table 3). Of the 44 species of non-vascular plants, 27 appeared between years 3 and 10 post-fire as canopy and understorey cover increased.

(d) *Dominant species.* The proportion of tree and shrub species was similar for both open-forest and gully complexes. However, open-forest contained more grass, lily, orchid and other

herbaceous species than gully complexes, which contained more species of liverworts, ferns and sedges (Table 3).

Eucalyptus tricarpa was the dominant eucalypt

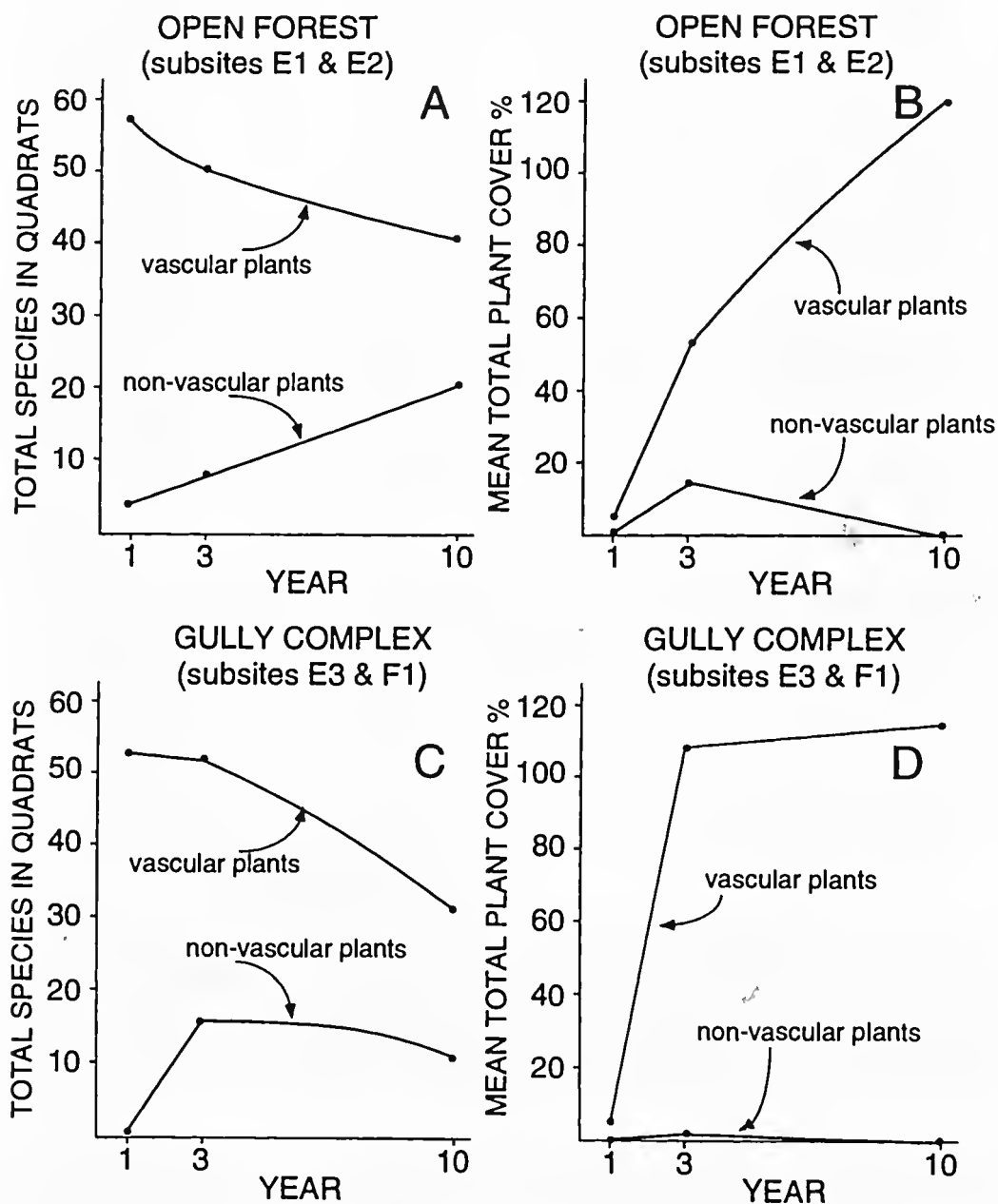


Fig. 2. Species richness and plant cover (%) at 1, 3 and 10 years post-fire. A, Species richness in open-forest (subsites E1 and E2 combined). B, Cover (%) in open-forest (subsites E1 and E2 combined). C, Species richness in gully complex (subsites E3 and F1 combined). D, Cover (%) in gully complex (subsites E3 and F1 combined).

of the open-forest communities (subsites E1 and E2). On the north facing slope (subsite E1—Fig. 3) it comprised 87% of all trees in the total population (690 stems/ha), and occurred as single-trunked trees mean 18.2 m tall (SD 2.82, range 14.6–22.8 m) of girth 97.4 cm (SD 20.2). On the south-facing slope (subsite E2) it comprised 80% of all trees in the total population (1000 stems/ha), again occurring as single-trunked trees mean 17.2 m tall (SD 3.4, range 12.4–22.6 m), of girth 108 cm (SD 42).

Gully complexes were dominated by *Eucalyptus cypellocarpa* at subsite E3, and *Eucalyptus obliqua* at subsite F with a density of 10–20 trees/ha (subsite F1—Fig. 4). The *E. cypellocarpa* at subsite E3 were large old single-trunked trees 30–35 m tall and of GBH >1.5 m. The *E. obliqua* at site F (and in the open-forest surrounding site F) were smaller, single trunked trees approximately 14–22 m tall and of GBH approximately 1.0–1.5 m.

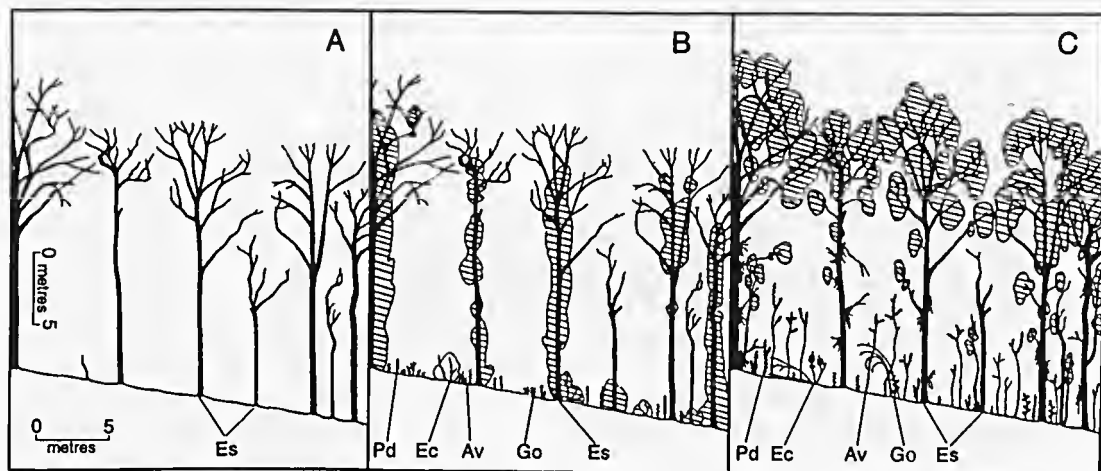


Fig. 3. Vegetation profiles in open-forest (subsite E1) immediately after the fire and 3 and 10 years later. Horizontal and vertical scales are the same. Hatching indicates the extent of canopy regrowth. A, Open-forest of *Eucalyptus tricarpa* (Es) immediately after the fire. B, 3 years after fire. Small coppicing trees of *Eucalyptus cypellocarpa* (Ec); *Pultenaea daphnoides* (Pd), *Acacia verticillata* (Av) and *Goodenia ovata* (Go) are present in the shrub stratum. C, 10 years after fire.

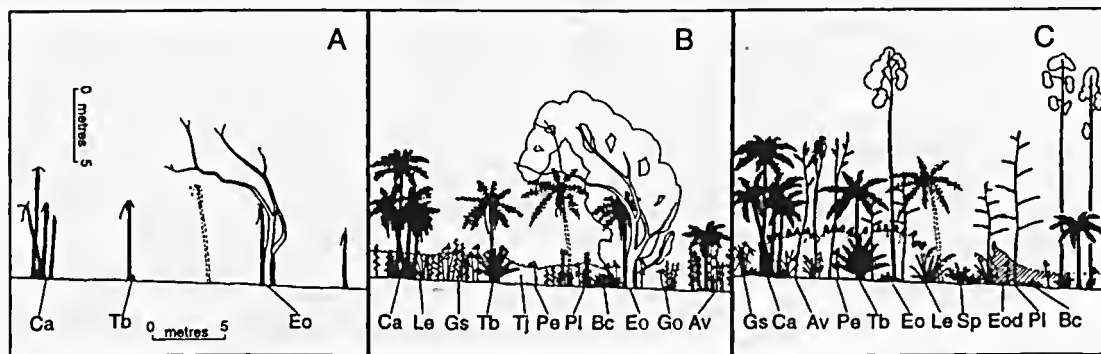


Fig. 4. Vegetation profiles in a gully complex (subsite F1) immediately after the fire and 3 and 10 years later. Horizontal and vertical scales are the same. A, *Eucalyptus obliqua* (Eo) gully complex immediately after the fire with *Cyathea australis* (Ca) and *Todea barbara* (Tb) present in the understorey. B, 3 years after fire. *Lepidosperma elatius* (Le), *Galinia sieberiana* (Gs), *Tetrarrhena juncea* (Tj), *Pteridium esculentum* (Pe), *Prostanthera lasianthos* (Pl), *Goodenia ovata* (Go), *Acacia verticillata* (Av) and *Blechnum cartilagineum* (Bc) are present in the understorey. C, 10 years after fire. *Spyridium parvifolium* (Sp) and dead *Eucalyptus obliqua* (Eod).

Subsite Vegetation type	E1 Open forest	E2 Open forest	E3 Gully complex	F1 Gully complex	F2 Modified gully complex
Eucalypts* (species)	Et	Et Ec Ea Ew Eo	Ec	Eo	Eo Ew
Cover %					
Prefire (approx.)	30-70	30-70	30-70	30-70	30-70
3 years	<10	<10	30	30	70
10 years	30-70	30-70	30-70	30-70	70
Height (m)					
Prefire (approx.)	18.2	17.2	36.0	14.0	14.0
Live stem height after fire (Year 0)	14.2	13.2	30.0	12.0	0.0
3 years	14.6	13.9	32.0	14.0	5.0
10 years	16.8	16.5	34.0	14.1	18.0
Length of Epicormics (m)					
3 years { Base	0.80	0.52	—	—	—
Trunk	0.45	1.33	3.5	3.0	—
Crown	0.94	0.90	2.5	2.5	—
Understorey					
Cover %					
Prefire (approx.) - all plants	10-30	30-70	30-70	30-70	30-70
3 years { shrubs	25.0	25.0	30.0	10.0	1.0
moss	—	30.0	1.0	1.0	1.0
ferns	—	—	38.5 [‡]	19.7 ^{§,‡,!}	10.0 [‡]
all plants	26.5	62.5	>82.5	77.5	15.0
bare ground	73.5	37.5	<17.5	22.5	85.0
10 years { trees (<4 m)	—	—	tr	—	tr
shrubs	60.0 [§]	50.0 [§]	50.0	10.0	tr
sedges/rushes	tr	15.0	tr	5.0	2.0
grasses	tr	15.0	30.0	—	1.0
other herbs	tr	tr	tr	— tr	tr
ferns	—	—	tr	45.0 —	1.0
mosses etc	tr	tr	tr	tr	1.0
all plants	60.0	80.0	80.0	50.0	5.0
litter	20.0	20.0	20.0	40.0	75.0
bare ground	20.0	—	—	—	20.0
Height (m)					
Prefire (approx.)	3.0	3.0	3.0 ^Φ	4.5 ^δ , 5.5 [†]	4.5 ^δ , 5.5 [†]
Live stem height after fire (Year 0)	0.00	0.00	0.00	4.5 ^δ , 0.0 [†]	0.0, 0.0
3 years	2.0	2.5	2.0 [‡]	4.5 ^δ , 1.0 [†]	1.8 [‡]
10 years	3.8 [§]	4.2 [§]	6.0 ^Φ	5.3 ^δ , 5.9 [†]	2.0 [‡] , 1.8 [‡]

Table 4. Structure of forest and gully plant communities 3 and 10 years after fire. *Tallest stratum, Et=*Eucalyptus tricarpa*, Ec=*Eucalyptus cypellocarpa*, Ea=*Eucalyptus aromaphloia*, Ew=*Eucalyptus willisii*, ^Φ=*Pomaderris aspera*, [†]=*Prostanthera lasianthos*, ^δ=*Cyathea australis*, [!]=*Todea barbara*, [‡]=*Pteridium esculentum*, [‡]=*Spyridium parvifolium*, [§]=*Acacia verticillata*, tr=trace.

(e) *Introduced species.* Eleven introduced species were present at low density either near creeks (subsites E3, F1 and F2; *Aster subulatus*, *Briza minor*, *Sonchus oleraceus*), close to roads (subsites E1 and E2; *Anthoxanthum odoratum*, *Hypochoeris radicata*, *Stellaria media*, *Vulpia myuros*) or both (subsites E1, E2, E3, F1 and F2; *Aira caryophylla*, *Isolepis hystrix*, *Centaurium spicatum*, *Cirsium vulgare*).

(f) *Non-vascular plants.* In all communities, non-vascular plants were common colonizers of bare ground in the first 6 months after fire. They established apparently from wind-borne spores, growing in areas where the upper 2 cm of ash-rich surface soil had not been removed by wind or sheet erosion. A definite sequence of species was seen which was particularly noticeable on damper southerly slopes of open-forest (subsite E2, Table 3) where whole hillsides were colonised by the liverwort *Marclantia berteriana* and the moss *Funaria hygrometrica* and the fungus *Gerronea postii* in the first 6–8 months after fire. During year 2, *F. hygrometrica* was replaced by another moss, *Ceratodon purpureus*, and then in year 3 by a greater variety of species including *Barbula calycina*, *Campylopus introflexus* and *Polytrichum juniperinum* (Table 3). A similar sequence of mosses was seen at drier forest sites (subsite E1), in gully complexes (subsites E3 and F1), and on burnt peat following initial colonisation by *M. berteriana* (Table 3).

By year 3, ground covered by bryophytes in Ironbark forest ranged from 10% on dry eroded north facing slopes (subsite E1) to 25–75% in damper south facing slopes (subsite E2, Table 4).

Structure. At all sites, the fire completely incinerated the understorey and crown fired the overstorey, killing the top 4.0 m of the *E. tricarpa* canopy on the upper slopes and the top 6.0 m and 2.0 m of the *E. cypellocarpa* and *E. obliqua* canopies in the gullies. Very small trees (girth <35 cm) were burnt to the ground. Some 4–6 m trees of the understorey were killed above ground then produced root suckers (eg. *Exocarpos cupressiformis*, *Acacia melanoxylon*); others (eg. *P. lasianthus*) were completely killed.

The overstorey and understorey at all sites began to re-establish in the first year after fire (Table 4, Figs 3–6).

(a) *E. tricarpa open-forest* (subsites E1 and E2; Table 4, Figs 3, 5A, 6A). Ninety per cent of eucalypt individuals survived the fire and vegetative regrowth commenced within 2–3 months. *E. tri-*

carpa of GBH greater than 0.5 m pre-fire sprouted from epicormic buds at the base or trunk, whereas trees of less than 0.2 m GBH sprouted from the base only. No significant changes in girth were observed in the first 3 years after fire. In open-forest communities during years 1–3, basal epicormics of eucalypts contributed significantly to vegetation cover and were more common on trees on dry, upper northerly facing slopes, than in moister sites.

Rate of recovery of *E. tricarpa* canopy height and cover (relative to approximate original height and cover) was slower than that of the eucalypts in the gully complexes (Table 4, Figs 3, 4).

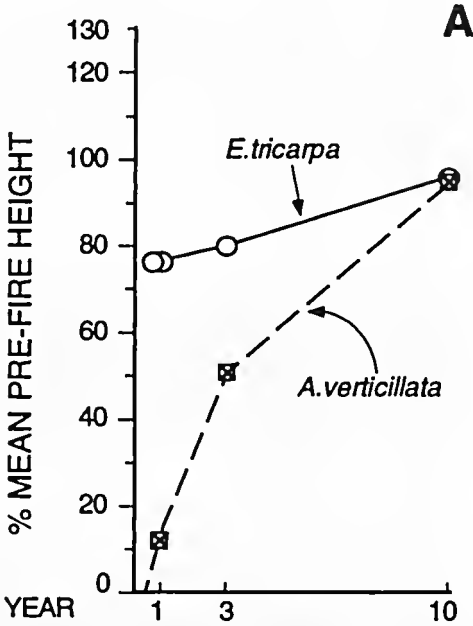
Crown recovery was slow in *E. tricarpa* open-forest; almost no canopy regrowth was seen by year 3 (Table 4, Fig. 3). By year 10, the eucalypt overstorey had recovered reaching approximate pre-fire height and estimated cover values (Table 4, Figs 3, 5A). Density of seedling eucalypts at subsites E1 and E2 was 3000–6000/ha 8 months after the fire, 200–600/ha 3 years after the fire, and approximately 100/ha 10 years after fire.

The understorey of the *E. tricarpa* open-forest communities (site E), changed in both structure and species composition following the fire. Prior to the fire the understorey in most of the forest had been open, grassy and dominated by *Poa sieberiana* (Parsons et al. 1977; Wark, pers. obs.). A few senescent shrubs of hard-seeded species such as *Acacia verticillata* and *Pultenea daplinoidea* were found on the lower slopes near creeks. Following the wildfire, massive germination of seedlings of *A. verticillata*, *P. daplinoidea* and *Goodenia ovata* occurred during year 1 at site E. This germination produced two crops of seedlings at approximately 2–6 and 12–18 months, seedlings establishing among the carpets of mosses and liverworts on the thin top soil that remained following soil erosion.

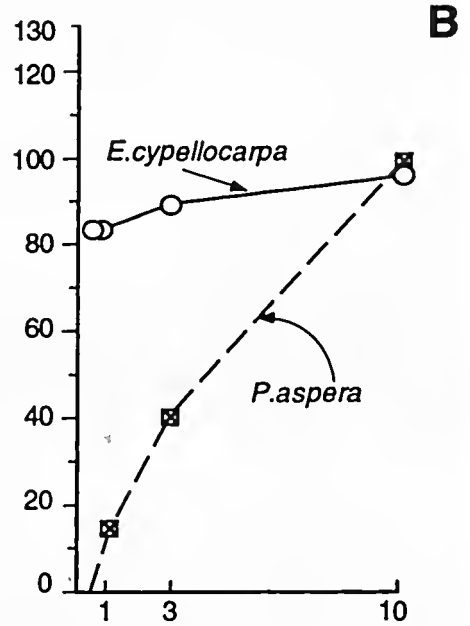
The new shrub layer grew rapidly in the early years after fire, and by year 3 formed a dense, prickly, understorey. It reached approximately 4.0 m by 10 years (Table 4, Figs 3, 5A, 6A), becoming spindly and senescent by 13 years. By year 10, the three main shrubs, *Acacia verticillata*, *Goodenia ovata* and *Pultenea daplinoidea*, had reached heights of 3.8 m, 1.4 m and 1.9 m respectively at subsite E1.

The grassy (*Poa sieberiana*) understorey, seen pre-fire, did not reappear in the 10 years after the fire. However, on damper southerly slopes, on silty clay (subsite E2), wire grass (*Tetrarrhena juncea*) and thatch saw-sedge (*Gahnia radula*) re-established, and were significant cover components during the 10 years (Fig. 6A).

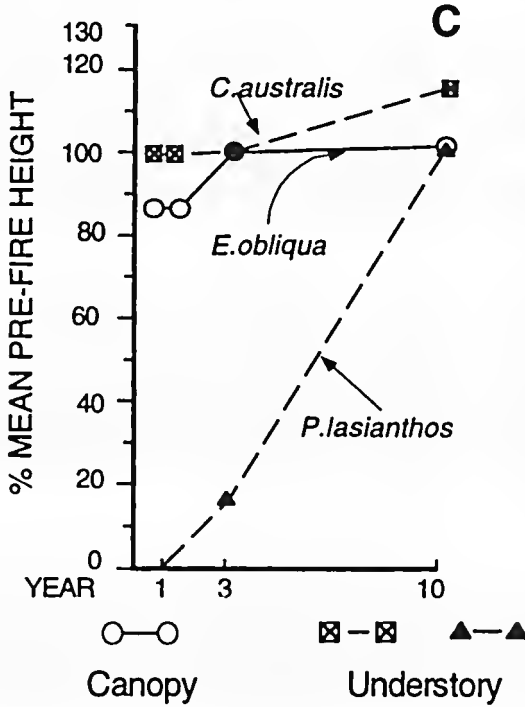
COMMUNITY: Open forest
SUBSITE: (E1, E2)



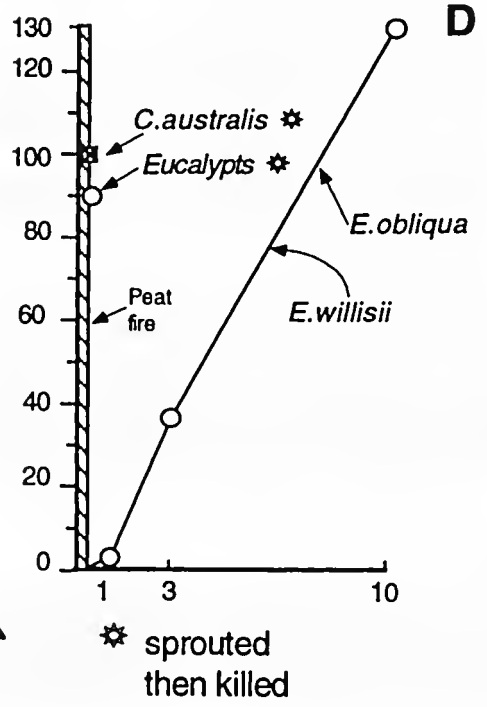
Gully complex
(E3)



COMMUNITY: Gully complex
SUBSITE: (F1)



Modified gully complex
(F2)



In open-forest the number of herbaceous species present decreased during the 10 years to 43% of the year 1–3 level (97 years 1–3; cf. 42 year 10, Table 3).

(b) *Gully complexes* (subsites E3 and F1; Table 4, Figs 4, 5B, 5C, 6B, 6C). About 90% of eucalypts in gully complexes survived the fire. Regrowth of 36.0 m tall *Eucalyptus cytellocarpa* (GBH pre-fire >1.5 m) and 14.0 m tall *E. obliqua* (GBH pre-fire >1.0 m) was by epicormic regrowth from the crown and upper branches; crown recovery occurring by 10 years (Table 4, Figs 4, 5B, 5C). Surviving *E. cytellocarpa* of GBH <0.4 m sprouted from the base only. At subsite F1, two 14.0 m *E. obliqua* sprouted following the fire, grew vigorously for 3 years, then fell (Fig. 4).

At subsite F1, 92% of *Cyathea australis* (5.0 m tall; range 4.5–6.0 m) survived the fire and sprouted from the crown 3 weeks post-fire, growing 0.8 m in the 10 years post-fire (Figs 4, 5C).

At subsite E3 the previous understorey of *Pomaderris aspera* and *Prostanthera lasianthos* re-established from seed in the 10 years after fire (Table 4, Fig. 5B). Similarly, at subsite F1, the *P. lasianthos* understorey re-established in the 10 years reaching approximate pre-fire height and cover (Table 4, Fig. 5C). By year 10, the mean height of seedling shrubs of *P. lasianthos* at subsite F1 was 5.9 m (range 4.9–9.0 m). At both sites, *Pteridium esculentum* contributed significantly to substratum cover in years 1–3, then was rarely seen (Figs 6B, 6C). *Tetrarrhena juncea* was also a significant cover component till

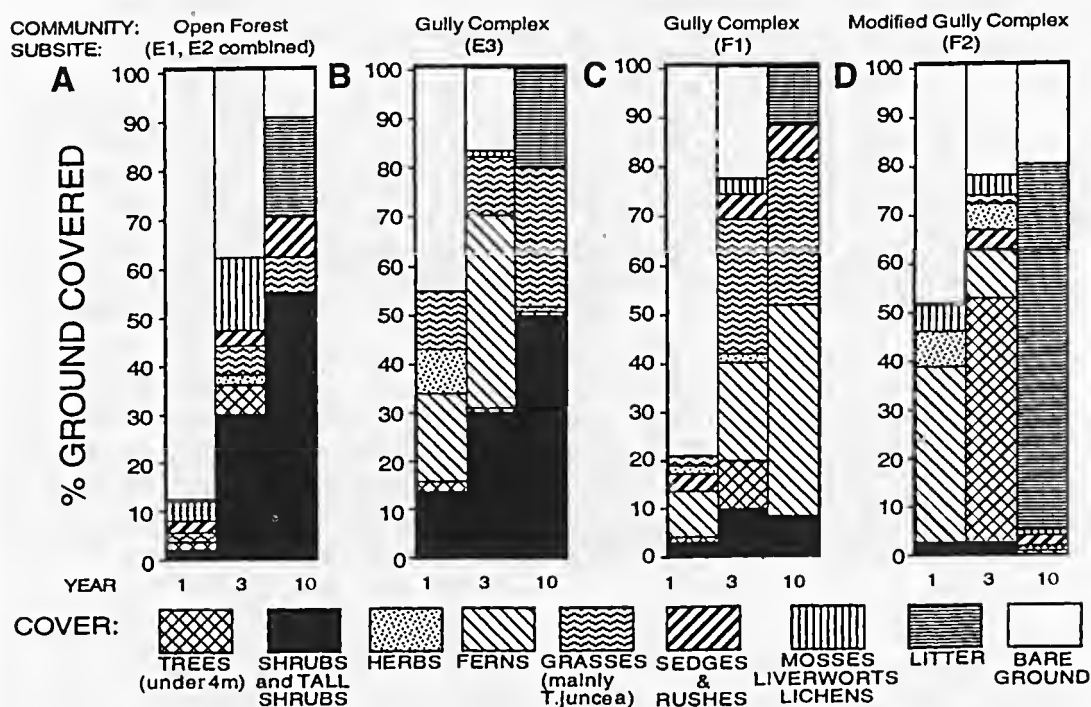


Fig. 6. Cover of shrub stratum and ground stratum of open-forest and gully complexes 1, 3 and 10 years after fire. *Tetrarrhena juncea* (*T. juncea*). A, Open-forest (subsites E1 and E2 combined). B, Gully complex (subsite E3). C, Gully complex (subsite F1). D, Modified gully complex (subsite F2).

Fig. 5. Recovery of height of the tree stratum (canopy) and shrub stratum (understorey) 1, 3 and 10 years after fire. A, Open-forest (subsites E and E2 combined). *E. tricarpa*=*Eucalyptus tricarpa*; *A. verticillata*=*Acacia verticillata*. B, Gully complex (subsite E3). *E. cytellocarpa*=*Eucalyptus cytellocarpa*; *P. aspera*=*Pomaderris aspera*. C, Gully complex (subsite F1). *E. obliqua*=*Eucalyptus obliqua*; *C. australis*=*Cyathea australis*; *P. lasianthos*=*Prostanthera lasianthos*. D, Modified gully complex (subsite F2). *E. obliqua*=*Eucalyptus obliqua*; *E. willisii*=*Eucalyptus willisii*; *C. australis*=*Cyathea australis*.

year 10, growing vigorously in sunny areas (Figs 6B, 6C). The filmy fern, *Hymenophyllum cupressiforme*, recorded at subsite F1 before the fire, was not seen in the 10 years post-fire.

Eucalypt seedlings germinated in open areas at subsite F1, reaching densities of 14 000/ha at year 3, and 140/ha at year 10, and mean height of 5.0 m and 18.0 m at years 3 and 10 respectively. Seedlings shaded by *Cyathea australis* or *Todea barbara* reached only a height of 2.0 m by year 3, and did not survive till year 10. In contrast, at subsite E3, where conditions were drier and *P. esculentum* cover denser, eucalypt seedling density at years 3 and 10 years was 200/ha and approximately 20/ha respectively.

(c) *Modified gully complex* (subsite F2; Table 4; Figs 5D, 6D). Major structural changes were observed at this subsite when a peat fire was ignited by the Ash Wednesday wildfire and continued to burn for 3 months. Mature 5.0 m tall *Cyathea australis* and 14.0 m tall *Eucalyptus obliqua* which survived the wildfire and sprouted at 3 and 8 weeks respectively, were burnt by the peat fire, and died and fell at 3.0–3.5 months post-fire (when the *C. australis* fronds were 1.5 m long and the *E. obliqua* epicormic growth 0.3 m in length; Fig. 5D).

Death of regenerating plants following the peat fire resulted in a dry open sunny area. *Pteridium esculentum* invaded the site (from the unburnt peat at subsite F1) and with fire mosses dominated the area by year 1. Many eucalypt seedlings germinated in this open area during year 1, covering the site, and seedling density at 3 and 10 years was 37 000/ha and 10 000/ha respectively. The two main species present at year 3 were *E. obliqua* (20 000/ha) and *Eucalyptus willisii* (17 000/ha). The young plants grew rapidly, reaching a mean height of 5.0 m by year 3 and 18.0 m (GBH 82 cm) by year 10 (Table 4). By year 10, the eucalypt seedling population had formed a new overstorey, replacing the *Eucalyptus obliqua* and *E. willisii* killed by the peat fire (Fig. 5D). The understorey beneath these trees was extremely simple and sparse (5% cover) and contained little *P. esculentum*, little moss and an occasional shrub (Fig. 6D).

The previous understorey of *Cyathea australis* and *Prostanthelia lasianthos* never re-established during the 10 years post-fire (Fig. 5D). Only two plants of *P. lasianthos* 5.0 m tall and one plant of *C. australis* 0.1 m tall were found at the site at year 10.

Though understorey cover of vascular and non-vascular plants on the burnt peat (subsite F2)

3 years post-fire was approximately the same as that of the adjacent gully community (subsite F1), total species richness at subsite F2 (years 1–3 combined) was 45% of that at subsite F1. By year 10, total understorey plant cover at subsite F2 was about 5%, and total plant species richness about 60% of that in the adjacent gully complex.

A total of 14 species of vascular plants and 12 species of bryophytes (mainly mosses) were found on the burnt peat at year 10 (Table 3). Fallen trees and tree ferns, killed by the peat fire, formed a tangled layer of litter (Table 4, Fig. 6D). Most bryophyte growth was on charred, fallen trunks of dead eucalypts or *C. australis*, rather than on the burnt peat, which by 10 years was covered by a 2 cm layer of humus and dead leaves.

Regeneration strategies

(a) *Regeneration mechanisms and timing.* Regeneration was either by regrowth (from dormant buds, in stems, lignotubers, root tussocks, roots, rhizostolons, rhizomes, corms, tubers and tuberoles) from seed or propagules, or by both means (Table 5).

The first species to appear following the fire regenerated mainly by regrowth and included the ferns *Cyathea australis*, *Pteridium esculentum* and *Todea barbara* at three weeks, and sedges, rushes and other herbaceous species from four to five weeks. Regrowth of eucalypts commenced between two to three months. As mentioned earlier, the fire moss *Funaria hygrometrica*, the liverwort *Marchantia berteroana*, and fruiting bodies of the fungus *Gerronema postii* appeared 6–8 months after the fire, often forming extensive carpets on sheltered, damper slopes.

The three most conspicuous shrubs (*Acacia verticillata*, *Goodenia ovata* and *Pultenaea daphnoides*) germinated from seed between 2 and 6 months; and both north and south facing slopes in the ironbark forest looked like giant seed beds. By the end of year 1, all species capable of vegetative regrowth, and three-quarters of species which regenerated from seed, had appeared.

(b) *Regeneration strategies and life form groups.* Regeneration strategies and life form groups of all vascular species present 1–3 years post-fire and surviving till year 10 are shown in Table 6.

About 26% of vascular plant species regenerated only by regrowth (ORR) including sedges, rushes, lilies, orchids and Droseraceae. About 38% re-

Obligate seed regenerators [†] (from seed or spores or propagules only)			Facultative regrowth regenerators [†] (by regrowth, and from seed or propagules)		
	Regen. strategy	First flowering		Regeneration strategy	First flowering
Tall shrubs			Trees		
<i>Acacia dealbata</i>	S1		<i>Eucalyptus aromaphloia</i>	St1, L1	S1
<i>Acacia mearnsii</i>	S1		" <i>baxteri</i>	St1, L1	S1 F2
<i>Acacia pycnantha</i>	S1	F2	" <i>cypellocarpa</i>	St1, L1	S1
<i>Pomaderris aspera</i>	S1		" <i>globulus</i>		
<i>Pomaderris elachophylla</i>	S1	F3	" ssp. <i>bicostata</i>	St1, L1	S1
<i>Pomaderris ferruginea</i>	S1		" <i>obliqua</i>	St1, L1	S1 F2
<i>Prostanthera lasianthos</i>	S1		" <i>ovata</i>	St1, L1	S1
			" <i>tricarpa</i>	St1, L1	S1 F3
Lichens			" <i>viminalis</i>	St1, L1	S1
<i>Cladia aggregata</i>	S2		" <i>willisii</i>	St1, L1	S2 F3
Liverworts			Tall shrubs		
<i>Asterella drummondii</i>	S3	F3	<i>Acacia melanoxylon</i>	Rsk1, L1	S1
<i>Anthoceras laevis</i>	S3	F3	<i>Exocarpos cupressiformis</i>	Rsk1, L1	S1
<i>Cephalozia exiliflora</i>	S3	F3			
<i>Lethocolea pansa</i>	S3	F3	Ferns & allies		
<i>Lophocolea semiteres</i>	S3	F3	<i>Adiantum aethiopicum</i>	R1	S2 F2
<i>Marchantia polymorpha</i>	S1	F1	<i>Blechnum cartilagineum</i>	R1	S2 F2
<i>Symphygyna podophylla</i>	S3	F3	" <i>nudum</i>	R1	S2
Mosses			<i>Cyathea australis</i>	R1	S2 F1
<i>Barbula calycina</i>	S3	F3	<i>Gleichenia microphylla</i>	R1	S2 F2
<i>Bryum billardiieri</i>	S3	F3	<i>Hymenophyllum cupressiforme</i> ‡	?	? ?
" <i>pachytheca</i>	S3	F3	<i>Hypolepis rugosula</i>	R1	S2 F2
<i>Breutelia affinis</i>	S3	F3	<i>Pteridium esculentum</i>	R1	S2 F2
<i>Campylopus introflexus</i>	S3	F3	<i>Todea barbara</i>	R1	S2 F1
" <i>pyriformis</i>	S3	F3			
<i>Ceratodon purpureus</i>	S2	F2	Grasses		
<i>Funaria hygrometrica</i>	S1	F1	<i>Agrostis avenacea</i>	R1	S1 F1
<i>Polytrichum juniperinum</i>	S3	F3	* <i>Anthoxanthum odoratum</i>	R1	S1 F1
<i>Wijkia extenuata</i>	S3	F3	<i>Austrostipa rudis</i>	R1	S1 F1
Grasses			" <i>semibarbata</i>	R1	S1 F1
* <i>Aira caryophylla</i>	S1	F1	<i>Danthonia geniculata</i>	R1	S1 F1
* <i>Briza minor</i>	S1	F1	" <i>induta</i>	R1	S1 F1
<i>Echinopogon avatus</i>	S1	F1	" <i>pilosa</i>	R1	S1 F1
* <i>Vulpia myuros</i>	S1	F1	" <i>procera</i>	R1	S1 F1
			" <i>setacea</i>	R1	S1 F1
Shrubs			<i>Deyeuxia densa</i>	R1	S1 F1
<i>Acacia acinacea</i>	S1	F3	" <i>quadrisseta</i>	R1	S1 F1
" <i>genistifolia</i>	S1	F3	<i>Dichelachne rara</i>	R1	S1 F1
" <i>mucronata</i>	S1	F3	* <i>Halchus lanatus</i>	R1	S1 F1
" <i>myrtifolia</i>	S1	F3	<i>Joycea pallida</i>	R1	S1 F1
" <i>verniciiflua</i>	S1	F3	<i>Microlaena stipoides</i>	R1	S1 F1
" <i>verticillata</i>	S1	F3	<i>Notodanthonia semiannularis</i>	R1	S1 F1
<i>Correa reflexa</i>	S1	F2	<i>Tetrarrhena distichophylla</i>	R1	S1 F1
<i>Epacris impressa</i>	S1	F2(?)	" <i>juncea</i>	R1	S1 F1
<i>Gaodenia ovata</i>	S1	F1	<i>Poa marrisii</i>	R1	S1 F1
<i>Ozothamnus ferrugineus</i>	S1	F2	" <i>sieberiana</i>	R1	S1 F1
<i>Indigofera australis</i>	S1	F2	" <i>tenera</i>	R1	S1 F1
<i>Olearia lirata</i>	S1	F2(?)			
" <i>phlogopappa</i>	S1	F2	Shrubs		
" <i>ramulosa</i>	S1	F2	<i>Acrotriche serrulata</i>	L1	S1 F2
			<i>Astroloma humifusum</i>	L1	S1 F2

Table 5 continued next page (see legend on page 29)

Obligate seed regenerators † (from seed or spores or propagules only)			Facultative regrowth regenerators † (by regrowth, and from seed or propagules)		
	Regen. strategy	First flowering		Regeneration strategy	First flowering
" <i>teretifolia</i>	S1	F2	<i>Bursaria spinosa</i>	L1	S1 F2
<i>Pultenaea daphnoides</i>	S1	F2	<i>Coprosma quadrifida</i>	L1	S1
" <i>scabra</i>	S1	F2	<i>Hibbertia riparia</i>	L1	S1 F2
<i>Pimelea humilis</i>	S1	F1	<i>Lissanthe strigosa</i>	L1	S2 F2
" <i>linifolia</i>	S1	F2	<i>Lomatia ilicifolia</i>	L1	S1 rare F1
<i>Leptospermum continentale</i>	S2	F2?	<i>Melaleuca squarrosa</i>	L1	S1 rare F2?
<i>Solanum laciniatum</i>	S1	F2	<i>Olearia argophylla</i>	L1	S2 F3?
<i>Spyridium parvifolium</i>	S1	F2			
Herbs			Herbs		
<i>Acaena novae zelandiae</i>	S1	F2	<i>Brunonia australis</i>	R1	S1 F1
<i>Amyema pendulum</i> ‡	?	?	* <i>Carduus tenuiflorus</i>	R1	S1 F1
<i>Asperula scoparia</i>	S1	F2	<i>Cynoglossum suaveolens</i>	R1	S1 F1
* <i>Aster subulatus</i>	S1	F1	<i>Goodenia lanata</i>	R1	S1 F1
* <i>Centaureum spicatum</i>	S1	F1 or F2	<i>Helichrysum leucopsidium</i>	R1	S1 F1
* <i>Cirsium vulgare</i>	S1	F1	" <i>scorpioides</i>	R1	S1 F1
<i>Dichondra repens</i>	S1	F2	<i>Lagenifera gracilis</i>	R1	S1 F1
<i>Geranium solanderi</i>	S1	F1	" <i>stipitata</i>	R1	S1 F1
<i>Euchiton involucratus</i>	S1	F2	<i>Leptorhynchus linearis</i>	R1	S1 F1
" <i>sphaericus</i>	S1	F2	" <i>squamatus</i>	R1	S1 F1
<i>Gonocarpus tetragynus</i>	S1	F1	* <i>Oxalis corniculata</i>	R1	S1 F1
<i>Galium binifolium</i>	S1	F2	<i>Pelargonium australe</i>	R1	S1 F1
<i>Geranium</i> spp.	S1	F2	<i>Plantago varia</i>	R1	S1 F1
<i>Hydrocotyle callicarpa</i>	S1	F1	* <i>Sonchus oleraceus</i>	R1	S1 F1
" <i>hirta</i>	S1	F2?	<i>Veronica calycina</i>	R1	S1 F1
" <i>laxiflora</i>	S1	F2?	<i>Veronica derwentiana</i>	R1	S1 F2
<i>Hypericum gramineum</i>	S1	F1			
<i>Lobelia rhombifolia</i>	S1	F1	Obligate regrowth regenerators † (by regrowth only)		
<i>Opercularia varia</i>	S1	F1		Regeneration strategy	First flowering
<i>Phyllanthus gunnii</i>	S2?	F3?			
<i>Poranthera microphylla</i>	S1	F1			
<i>Rorippa dictyosperma</i>	S1	F1	Sedges & rushes		
<i>Senecio velleioides</i>	S1	F2	<i>Gahnia radula</i>	R1	F2
<i>Senecio</i> spp.	S1	F1	" <i>sieberiana</i>	R1	F2
<i>Stellaria flaccida</i>	S1	F1	* <i>Isolepis hystrix</i>	R1	F1
" <i>pungens</i>	S1	F2	" <i>indundata</i>	R1	F1
" <i>media</i>	S1	F2?	" <i>marginata</i>	R1	F1
<i>Viola hederacea</i>	S1	F1	<i>Juncus pauciflorus</i>	R1	F2
" <i>cleistogamoides</i>	S1	F1	" <i>planifolius</i>	R1	F1
<i>Wahlenbergia gracilienta</i>	S1	F1	<i>Lepidosperma elatius</i>	R1	F2
" <i>stricta</i>	S1	F1	<i>Luzula meridionalis</i>	R1	F1
			<i>Schoenus apogon</i>	R1	F1
Creepers & climbers			Orchids		
<i>Billardiera scandens</i>	S1	F2	<i>Acianthus caudatus</i>	Tu1	F1
<i>Cassytha glabella</i>	S1	F2	" <i>pusillus</i>	Tu1	F1
" <i>melantheria</i>	S2	F2	<i>Caladenia cardiophylla</i>	Tu1	F1
<i>Clematis aristata</i>	S1	?	<i>Caladenia catenata</i>	Tu1	F1
<i>Comesperma volubile</i>	S1	F1	" <i>tentaculata</i>	Tu1	F1
<i>Glycine clandestina</i>	S1	F2	" <i>menziesii</i>	Tu1	F1
<i>Kennedia prostrata</i>	S1	F1	" <i>reticulata</i>	Tu1	F1
			<i>Cyrtostylis reniformis</i>	Tu1	F1
			<i>Dipodium punctatum</i>	Tu1	F1
			<i>Eriochilus coccullatus</i>	Tu1	F1
			<i>Prasophyllum odoratum</i>	Tu1	F1

Table 5 continued next page (see legend on page 29)

Obligate regrowth regenerators [†] (continued) (by regrowth only)		
	Regeneration strategy	First flowering
<i>Pterostylis longifolia</i>	Tu1	F1
" <i>nutans</i>	Tu1	F1
" <i>nana</i>	Tu1	F1
" <i>parviflora</i>	Tu1	F1
" <i>sanguinea</i>	Tu1	F1
<i>Thelymitra flexuosa</i>	Tu1	F1
" <i>ixioides</i>	Tu1	F1
" <i>pauciflora</i>	Tu1	F1
" <i>rubra</i>	Tu1	F1
Lilies & irises		
<i>Burchardia umbellata</i>	T1	F1
<i>Caesia parviflorus</i>	T1	F1
<i>Dianella revoluta</i>	T1	F2
<i>Lomandra filiformis</i>	T1	F1
" <i>longifolia</i>	T1	F1
" <i>micrantha</i>	T1	F1
" <i>multiflora</i>	T1	F1
<i>Thysanotus juncifolius</i>	T1	F1
" <i>tuberosus</i>	T1	F1
" <i>pateronii</i>	T1	F1
Herbs		
<i>Drosera peltata</i>		
ssp. <i>auriculata</i>	T1	F1
" <i>macrantha</i>	T1	F1
" <i>peltata</i>	T1	F1
" <i>whittakerii</i>	R1	F1
* <i>Hypochoeris radicata</i>	R1	F1
<i>Lobelia gibbosa</i>	R1	F1

Table 5. Regeneration strategies and flowering of forest and gully communities 1–3 years after fire. Key: Regeneration strategy/year—S1=germinated from seed year 1; S2=germinated from seed year 2; S3=germinated from seed year 3; R1=regrowth from rhizomes year 1; R2=regrowth from rhizomes year 2; T1=regrowth from tubers year 1; Tu=regrowth from tuberoids year 1; L1=regrowth from lignotubers year 1; St1=regrowth from stems year 1; C1=regrowth from coorns year 1; RSt1=regrowth from rhizostolons year 1; Rsk1=regrowth from root suckers year 1. Flowering/year—F1=first flowered year 1; F2=first flowered year 2; F3=first flowered year 3. [†]Terminology follows Purdie (1977a, 1977b). Seed is used to mean both seeds and spores. †=Present before fire, but not recorded 1–10 years after fire.

generated only from seed (OSR species) and were mainly shrubs and herbs. The remaining 36% were FRR species, regenerating both by regrowth and from seed, and included all trees, as well as shrubs, ferns and herbs (Table 6).

Approximately 62% of all vascular species which appeared in the first 3 years were sprouting species (ORR and FRR; Table 6). The other 38% were, as mentioned earlier, OSR species. A similar proportion (40%) of OSR species remained at year 10, in fact about 73% of all shrub species present at years 1–3 and remaining till year 10 were OSR (29 of 40, years 1–3; 24 of 33, year 10; Table 6).

About 48% of herbaceous species and 83% of shrub species present immediately after fire were still present at year 10.

Aerial parasites such as *Amyema pendulum* did not reappear in the 10 years after the fire. Root parasites such as *Exocarpus cupressiformis* regenerated both vegetatively and from seed, but died between years 3 and 7.

(c) *Regeneration strategies of trees and shrubs.* About 40% trees and shrubs were FRR regenerators, including all eucalypt species (Table 5). Some FRR shrubs, such as *Acacia melanoxylon*, showed only small amount of rootstock regeneration germinating mainly from seed. Others, like *Exocarpos cupressiformis* and *Olearia argophylla*, regenerated in approximately equal numbers by regrowth (from lateral roots or the base of the trunk) or from seed. Species such as *Bursaria spinosa* regenerated mainly by regrowth. No shrubs regenerated by regrowth exclusively.

Sixty per cent of trees and shrubs regenerated from seed only. In the Ironbark forest, where a shrub layer had not been present in the years before the fire, densities of shrub seedlings 1 year after fire were *A. verticillata* 23 seedlings/m², *G. ovata* 25 seedlings/m², *P. daphnoides* 10 seedlings/m². Many of these seedling shrubs died during the dry summer period, and densities at year 3 were 10 seedlings/m², 9 seedlings/m², and 6 seedlings/m² respectively (100 000/ha, 90 000/ha, 60 000/ha).

(d) *Regeneration strategies on burnt peat.* With the exception of *Pteridium esculentum* and *Tetrarrhena juncea* (both of which invaded by rhizomes from outside), all species which established on the burnt peat (subsite F2) regenerated either from seed or spores. All 14 species of vascular plants which appeared on the burnt peat in the 10 years following the fire were present in either the adjacent gully complex (subsite F1) or the neighbouring 18–20 m tall *E. obliqua*/*E. willisii* heathy open-forest following the fire (eg. *Spyridium parvifolium*). One introduced species (*Aster subulatus*, present subsite F1) regenerated on the burnt peat in the 10 years following the fire.

Species present Regeneration strategy post fire	OSR	Years 1-3 FRR	ORR	OSR	Year 10 FRR	ORR
Trees (9)*	-	9	-	-	7	-
Shrubs (40)	29	11	-	24	9	-
Dicotyledon herbs (52)		29	16	6	12	6
Monocotyledon herbs (65)						4
Orchids (20)	-	-	20	-	-	9
Lilies & irises (10)	-	-	10	-	-	6
Grasses (25)	4	21	-	-	6	-
Sedges & rushes (10)	-	-	10	-	-	3
Creepers & climbers (7)	7	-	-	3	-	-
Ferns (8)	-	8	-	-	8	-
Subtotal	69	65	46	39	36	22
% Total species ^δ	38%	36%	26%	40%	37%	23%
Total species ^δ		180			97	

Table 6. Regeneration strategies and life form groups of all vascular plant species appearing 1-3 years post-fire and still present 10 years post-fire. Key: OSR=obligate seed regenerators; FRR=faeultative regrowth regenerators; ORR=obligate regrowth regenerators. Terminology follows Purdie (1977a, 1977b). *Numbers in parentheses show total species present years 1-3; ^δtotal species=total number of species recorded (quadrat and site data combined).

Flowering response after fire

(a) *Response during first spring.* Sixty per cent of species (94 of 157) which regenerated during year 1 flowered or produced spores (Table 5). Of these, 87 species were herbs. The rest included 2 ferns, 2 bryophytes, a fungus and 3 species of shrubs.

About 82% of all herbs recorded (including sedges, rushes, grasses, orchids, lilies, creepers and climbers) flowered in the first year after fire, and almost all the rest by year 2. Some ORR herbs, including autumn and winter-flowering orchids (*Acianthus pusillus*, *Eriochilus cucullatus*, *Pterostylis parviflora*), flowered from 5 months post-fire, as did *Drosera whittakeri* and *Lagenifera gracilis*.

There was conspicuous production of fruiting bodies by the moss *Funaria hygrometrica*, the liverwort *Marchantia berteroana*, and the fungus *Gerronema postii* from 6 months post-fire. By late spring, whole hillsides of the open-forest in damp areas (such as subsite E2) were coloured yellowish green by a carpet of fruiting bryophytes.

Grasses were conspicuous in the first spring after fire. Twenty-three species were identified at open-forest sites including 5 species of *Danthonia* (Table 3). Some species (eg. *Danthonia induta* and *D. procera*) flowered prolifically then were not seen in later years. Only 5 species of grasses were recorded in open-forest by year 10 (Table 3).

(b) *Orchid flowering response.* Nineteen species of terrestrial orchids appeared and flowered in

open-forest during the first 3 years after fire. Though 16 species of orchids were recorded at subsite E1 during the 10 years, only 4 species appeared and flowered on this dry, eroded slope during year 1 (Table 3). Field observations suggest that the density of year 1 flowering of most species was higher than in pre-fire years.

Flowering of some orchid species was stimulated by fire. Two species (*Caladenia menziesii* and *Prasophyllum odoratum*), which appear but rarely flower in normal years, bloomed prolifically the spring after the fire. Seed-set accompanied post-fire flowering for all orchid species during years 1–3.

Only 3 species of orchids (*Acianthus pusillus*, *Pterostylis nana*, *P. nutans*) were recorded in the gully communities prior to the fire and in the 10 years post-fire. Field records made in similar communities near Moggs Creek prior to the fire, list 11 gully species (*Acianthus caudatus*, *A. pusillus*, *Chiloglottis valida*, *Corybas dilatatus*, *C. incurvis*, *Cyrtostylis reniformis*, *Pterostylis curta*, *P. longifolia*, *P. nana*, *P. nutans*, *P. pedunculata*—M. White; M. MacDonald, pers. comm.), all of which have been observed in the 10 years post-fire.

(c) *Flowering response of trees and shrubs.* Three shrubs (*Goodenia ovata*, *Pimelea lunulilis*, *Lomatia ilicifolia*) flowered in the first year. All other shrubs (92%) did not commence flowering till years 2 or 3, or later (Table 5). *Lomatia ilicifolia* (which is rarely seen to flower except after fire) flowered on new regrowth at 6–8 months. The juvenile phase of some shrubs (eg. *Epacris impressa*, *G. ovata*) was brief; flowering occurring within 2 years on plants only a few centimetres high.

By year 3, about two-thirds of the vascular plant species had flowered, including 4 species of trees (*Eucalyptus baxteri*, *E. obliqua*, *E. tricarpa*, *E. willisii*) and 27 species of shrubs. Not flowering at year 3 were 5 species of trees (*Eucalyptus aromapholia*, *E. cypellocarpa*, *E. globulus*, *E. ovata*, *E. viminalis*), and 7 species of tall shrubs (*Acacia dealbata*, *A. mearnsii*, *A. melanoxyloa*, *Pomaderris aspera*, *P. ferruginea*, *Prostanthera lasiantha*, *Exocarpus cupressiformis*). All 12 species flowered by 10 years post-fire.

By year 3, the percentage of OSR shrubs and OSR herbs flowering was 83% and 97% respectively and most of these species appeared to set seed. Little seed predation was observed either on plants or the soil.

(d) *Grazing during first 3 years.* No grazing of

vegetation by native or introduced mammals was seen in the first 2.5 years after fire; though European rabbits (*Oryctolagus cuniculus*) were observed browsing herbs at subsite E1 late in year 3, and swamp wallabies (*Wallabia bicolor*) browsing shrubs at subsite E2 during years 7 and 10. Heavy grazing of young shrubs of *Goodenia ovata* by unidentified insect larvae occurred at all sites during years 1 and 2, with about 50% of the leaves being eaten. Extensive grazing of *E. cypellocarpa* coppice regrowth (by sawfly larvae, *Perga* sp.) was seen at subsite E2 during year 3.

DISCUSSION

This study has shown that, after a long fire-free interval, an *E. tricarpa* open-forest in the Anglesea-Aireys Inlet district was resilient to a single severe summer surface wildfire, supporting observations of Gill (1975, 1981) for dry sclerophyll forests in southern Australia.

The regeneration patterns of the open-forest community conform to the 'initial floristic composition' models of Egler (1954), and Purdie & Slatyer (1976), as 99% of vascular plant species present prior to fire re-established during the first three years.

The increase in the number of species of non-vascular plants in both open-forest and gully communities, with time, and as vascular plant cover increased, is similar to that recorded for the Anglesea heaths and heath woodlands (Wark 1996). The decrease in vascular plant species richness, as vascular plant projective cover increased, is similar to that described by Specht and Specht (1989) for sclerophyll communities in southern Australia, and was also observed in the heaths and heath woodlands of the Anglesea area (Wark 1996).

The failure of *Anyema pendulum* and *Hymenophyllum cupressiforme* to re-establish in the Ironbark forest and the gully communities respectively in the 10 years following the wildfire is not unexpected. All plants of *A. pendulum* were killed, and the mistletoe bird, *Dicaeum hirundinacium* (which is responsible for seed distribution and was uncommon in the Angahook-Lorne State Park before the fire—Conole & Baverstock 1984; Gill 1994), has not been seen in the area in the 10 years since 1983 (P. Reilly, pers. comm.; Reilly 1991). Filmy ferns such as *H. cupressiforme*, were rare in the district before the fire and probably have not re-established because the climate in the

gully complexes has become drier. It may take many years for a cool microclimate suitable for these delicate plants to develop. Ashton & Frankenberg (1976) and Chesterfield et al. (1991) have commented that *H. cupressiforme* is badly affected by wildfire. No *H. cupressiforme* plants were seen 5 years after the 1983 wildfire in warm temperate rainforest in East Gippsland, Victoria (Chesterfield et al. 1991), and only a few plants 25 years after the 1951 wildfire in cool temperate rainforest at Lily Pilly Gully, Wilsons Promontory National Park, Victoria (D. H. Ashton, pers. comm.).

In the *E. tricarpa* dry sclerophyll forest, 60% of all species which regenerated following this wildfire were sprouters (FRS or ORR species). Similar high proportions of vegetative regenerators have been described for dry sclerophyll forests in Western Australia (Christensen & Kimber 1975), and the Australian Capital Territory (Purdie & Slatyer 1976). The high proportion (40%) of OSR regenerators seen probably reflects the intensity of the wildfire. It is known that in dry sclerophyll forests in Western Australia and New South Wales high intensity fires stimulate germination of hard-seeded understorey shrubs and fireweeds (Christensen & Kimber 1975; Christensen et al. 1981; Auld & O'Connell 1991). The dense shrub understoreys (dominated by *Acacia* and *Pultenaea* spp.) which established throughout most of the open-forest communities of the Anglesea-Aireys Inlet region following the Ash Wednesday wildfire, replaced the previously more open, often grassy, understorey (Parsons et al. 1977). Field records (Pat Denham, pers. comm.) suggest that the seed which germinated forming the shrub understorey in the *E. tricarpa* open-forest may have been stored in the soil for over 30 years—possibly longer if previous fires were of insufficient intensity to stimulate germination.

The slow rate of crown recovery of the *E. tricarpa* open-forest in the first three years after fire, may have been a result of both moisture stress, and low nutrient status. Leitch et al. (1983) showed increased hydrophobic properties of the soil at a forest site near Warburton, Victoria, where extensive sheet erosion (and resulting soil nutrient losses) occurred following the Ash Wednesday wildfires. They commented that similar sheet erosion also occurred in some of the Otway forests following the Ash Wednesday fires, and our data supports this.

Both moisture and nutrients released from ash are necessary for establishment of early post-fire bryophyte colonisers such as *M. berteriana*, *F. hygrometrica* and *C. purpureus* (G. A. M. Scott,

pers. comm.; Crcmer & Mount 1965; Southorn 1977), and stimulate post-fire flowering in orchids (Pate & Dixon 1982). The reduced incidence of the early post-fire bryophytes at subsite E1, and the failure of 75% of the orchid species at this site to flower in the first year after fire, suggest that both moisture and certain nutrients were lacking in these exposed sites. In 1983, Barnett (1984) noted a decrease in flowering of some orchid species following a surface fire in a *Eucalyptus macrorhyncha* open-forest, on a steep site with heavy clay soils at King Lake, Victoria, and suggested that one factor which may have affected flowering was the removal, by soil erosion, of fire-released nutrients. Changes in the soil microflora after the fire may also have been a factor. Similarly, the failure of the parasitic tall shrub *E. cupressiformis* to survive on these dry sites after its early re-establishment from seed and by regrowth, suggests also that insufficient moisture and nutrients may have been available to the young plants in the early years after fire.

The open-forest described in the present paper may not be totally resilient to frequent severe wildfires if burning occurs before the primary juvenile period of some OSR species. In the Ironbark forest, 3 species of OSR tall shrubs (*Acacia mearnsii*, *A. dealbata*, *Pomaderris ferruginea*) had neither flowered nor set seed 3 years after the fire. If another fire occurred before they reached reproductive maturity, they could be eliminated. Parsons et al. (1977) have commented that repeated burning at frequent intervals may convert an open-forest with a shrub understorey to an open-forest with a grassy understorey. Coaldrake (1961) has observed similar changes following sequential fires in the coastal lowlands of southern Queensland.

In the gully complexes (where peat fires did not occur) 52% of the species which regenerated following the wildfire were OSR species, regenerating from seed only. Similar high proportions (50–60%) of obligate seed regenerators have been described for wet sclerophyll forests in Western Australia (Christensen & Kimber 1975), Victoria and New South Wales (Ashton 1981). The regeneration patterns of the Anglesea gully communities (in the absence of peat fires) also conformed to the initial floristic composition models of Egler (1954) and Purdie and Slatyer (1976) as 99% of vascular plant species present prior to the fire re-established during the first 3 years.

Like the *E. tricarpa* open-forest, the gully communities (where peat did not burn) may not be totally resilient to frequent severe wildfires.

By year 3, at least 4 OSR shrubs in each gully community had not flowered or set seed, including *Pomaderris aspera* and *Prostanthera lasianthos*. Seed of these species is stored in the soil, and *Pomaderris aspera* may be removed from an area if surface fires recur at intervals of less than 5–10 years (Ashton & Attiwill 1994). Burning of these areas twice within the primary juvenile period of these shrubs could result in their elimination.

The study has also shown that such dry gully communities may be extremely vulnerable to wildfire and that their floristics and structure may change dramatically if peat fires establish. In the 10 years following the peat fire, the *E. obliqua* gully complex with its *Prostanthera lasianthos*, *Cyathea australis* understorey has become a eucalypt monoculture with practically no understorey. It is likely that the seed source for recolonisation of the burnt peat was the surrounding *E. obliqua*/*E. willisii* open-forest, which contained 20 m eucalypts which had flowered and set seed the season before the wildfire. It was shown, after the Anglesea wildfires, that viable seed could survive in capsules of crown-fired *E. obliqua* (Ashton 1986). It is probable that seed shedding occurred onto the surface of the burnt peat after the in-ground fire was extinguished. Seeding in of *Spyridium parvifolium* probably also occurred from the surrounding open-forest. The presence of this shrub suggests the microclimate in both gully communities at site F is now drier than before the surface fire and the peat fire.

Hill & Read (1984) showed that the proximity of a sclerophyll seed source may result in significant changes in the species composition of the understorey of mixed eucalypt forests following humus fires in western Tasmania. They observed that species of sclerophyllous shrubs (*Leptospermum scoparium*, *Phebalium squameum*) found 150–400 m from their study area established from wind-dispersed seed on burnt peat.

In the present study it was found that, with the exception of two FRS species (*Pteridium esculentum*, *Tetrarrhena juncea*) which grew into the burnt peat after the fire ceased, all 12 other species of vascular plants found on the burnt peat at year 10 established from seed or spores shed into the area from the adjacent gully complex, or surrounding dry sclerophyll forest.

Because of the density of the eucalypt overstorey, and the changed hydrology of the area, it may be many decades, or even some hundreds of years, before an understorey of *Prostanthera lasianthos* and *Cyathea australis* re-establishes in the area of the peat fire. Burning of this area at 10 years, by

either a low intensity fire or a wildfire, could result in reduction or elimination of any OSR gully species which have begun to re-establish, and the continued invasion of sclerophyllous species from the adjacent *E. obliqua* open-forest.

It is probable that the red material produced when the peat burnt had certain properties which favoured plant establishment and growth in the short term. A dense cover of ash-requiring mosses and liverworts (including *F. hygrometrica*, *C. purpureus* and *M. berteriana*—Southorn 1977) appeared on the burnt peat in the first 3 years after fire. Cremer & Mount (1965) and Duncan & Dalton (1982) have described a similar sequence of bryophyte colonisation following felling and burning of *E. regnans* forests in Tasmania.

Pot experiments comparing burnt and unburnt peat showed that *E. obliqua* grew rapidly on burnt peat and then became chlorotic, probably due to nutrient imbalance or toxicity. Similar observations of chlorosis and poor growth have been made by Smith (1983) for *Acacia dealbata* growing on red burnt soils (derived from intense sustained log fires).

However, any nutrient imbalance of the burnt soil resulting from the peat fire did not prevent establishment of eucalypt seedlings, whose height at 3 years (5.0 m) equalled that of seedlings growing on unburnt peat in open areas, in the gully nearby. It is possible that increased light and a reduction of allelopathic factors in the soil, following burning of the peat, may have also contributed to the dense and rapid growth of eucalypt seedlings on the burnt peat. Once the seedlings on burnt peat (subsite F2) reached the 2.0 m water table (at 2–3 years), their growth appeared faster than that of seedlings on unburnt peat soil in the adjacent gully complex (subsite F1).

Though peat fires are relatively rare in mainland Australia (Gill 1981), the present study indicates that they may cause significant changes in vegetation structure and floristics in some gully communities. In the present study, no resilience was shown by an *E. obliqua*/*P. lasianthos*/*C. australis* gully community where a peat (ground) fire developed following a surface wildfire, as all the plants present at the time of the peat fire (including their buried seeds and propagules) were killed at or below ground level.

Similar lack of resilience has been reported following peat fires in *Melaleuca squarrosa* closed scrub on the humus-rich soil of the river valleys to the north and west of Anglesea with consequential changes in vegetation structure and floristics (Gill 1993; White 1994), and replacement

of the *M. squarrosa* closed scrub by a *Eucalyptus arnautophloia* woodland.

The present study indicates that, in Victoria, peat fires may occasionally cause significant changes in vegetation structure and floristics. Management strategies are required to prevent and control in-ground fires, especially when they establish in communities of ecological significance (Gill 1993, 1994).

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	Ross (1993)	Authority	Ross (1996)
Grasses	<i>Danthonia pallida</i> <i>Danthonia semiannularis</i> <i>Stipa rudis</i> <i>Stipa semibarbata</i>		<i>Joycea pallida</i> <i>Notodanthonia semiannularis</i> <i>Austrostipa rudis</i> <i>Austrostipa semibarbata</i>
Shrubs	<i>Hibbertia riparia</i> <i>Hibbertia stricta</i>		<i>Hibbertia riparia</i> <i>Hibbertia riparia</i>

Appendix. Nomenclature of vascular plants—name changes since the second paper in this series.

A LATE PERMIAN BRACHIOPOD FAUNA FROM SELONG, SOUTHERN XIZANG (TIBET), CHINA

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SHI, G. R. & SHEN SHU-ZHONG, 1997:11:30. A Late Permian brachiopod fauna from Selong, southern Xizang (Tibet), China. *Proceedings of the Royal Society of Victoria* 109 (1): 37-56. ISSN 0035-9211.

A brachiopod fauna from the middle part of the Selong Formation of the Selong Xishan (West Hills) section, southern Tibet is described and includes *Taeniothaerus* sp., *Chonetella nasuta* Waagen, *Lamnimargus himalayensis* (Diener), ?*Lamnimargus* sp., ?*Echinauris* sp., *Cleiothyridina* sp., *Posicomta grunti* sp. nov., *Spiriferella rajah* (Salter), *Neospirifer kubeiensis* Ting, *Trigonotreta* sp., and *Spiriferinacean* gen. et. sp. indet. This fauna is correlated with the *Lamnimargus himalayensis* Zone of the Himalayas. The age of the *Lamnimargus himalayensis* Zone is discussed and considered to be Midian to Early Dzhulfian (Late Permian).

PERMIAN marine strata are extensively distributed in Tibet, occurring in all the four major tectono-stratigraphic blocks (or terranes) (Fig. 1), and contain abundant invertebrate fossil remains. Brachiopoda are among the most abundant and diverse fossil groups present and have long been used as an important biostratigraphical tool for correlating the Permian marine sequences between the blocks and between Tibet in general and other Gondwanan regions. Biogeographically, Tibet is of particular interest because of its position between Eurasia to the north and Gondwana to the south. However, contention remains over the placement of the palaeobiogeographical boundary between the Gondwanan and Palaeo-Equatorial Realms (Sun 1993; Shi et al. 1995). This ongoing debate is in part due to insufficient knowledge of the stratigraphical and faunal relationships between the Tibetan blocks and between Tibet and Cathaysian and other Gondwanan regions.

A number of Permian brachiopod faunas have now been described from many isolated localities of southern Tibet (eg. Ting 1962; Zhang & Jin 1976; Jin & Sun 1981; Yang & Zhang 1982). Jin (1985) reviewed the faunas and established a biostratigraphical framework based on brachiopod assemblages. However, precise stratigraphical relationships among the previously described faunas remain to be clarified and detailed correlations of the Tibetan brachiopod faunas with known Himalayan brachiopod successions require refinement.

This paper describes a brachiopod fauna collected from near the Selong village in southern Tibet (Figs 1, 2) by one of the authors (SS-Z) in 1994. Zhang & Jin (1976) first described some brachiopod species from this section, but the detailed

stratigraphical positions of their collections were not specified. Recently, the Selong section has aroused considerable interest among geologists because of its potential as a global stratotype of the Permian-Triassic boundary (see Jin et al. 1996 and references therein provided). Most of the previous studies, however, have concentrated on the Permian-Triassic boundary beds and associated faunas, with little attention given to the faunas from the lower and middle parts of the Selong section.

STRATIGRAPHY

The name Selong Group was first proposed by the Scientific Investigation Team of the Chinese Academy of Science to Mt Xixiabangma in 1964 (unpublished; see Mu et al. 1973), with the type section at approximately 1 km northwest of the Selong village along the Tingri-Gyirong Highway, on the northern slope of Mt Xixiabangma (Fig. 2A). The unmeasured section was later described by Zhang (1974), with an estimated thickness more than 200 m assigned to the Permian. Rao & Zhang (1985) measured the type section and divided the Selong Group into two units: Mengdou Formation of Lower Permian, followed by the Baka Formation of Upper Permian, despite both formations of this section being characterised by bioclastic limestones with minor interbeds of shale and sandstones. Rao & Zhang (1985) also discovered a transitional or mixed fauna of Permian-Triassic character at the top of the Baka Formation and, as a consequence, suggested that the Selong section might represent a continuous Upper Permian to Lower Triassic sequence.

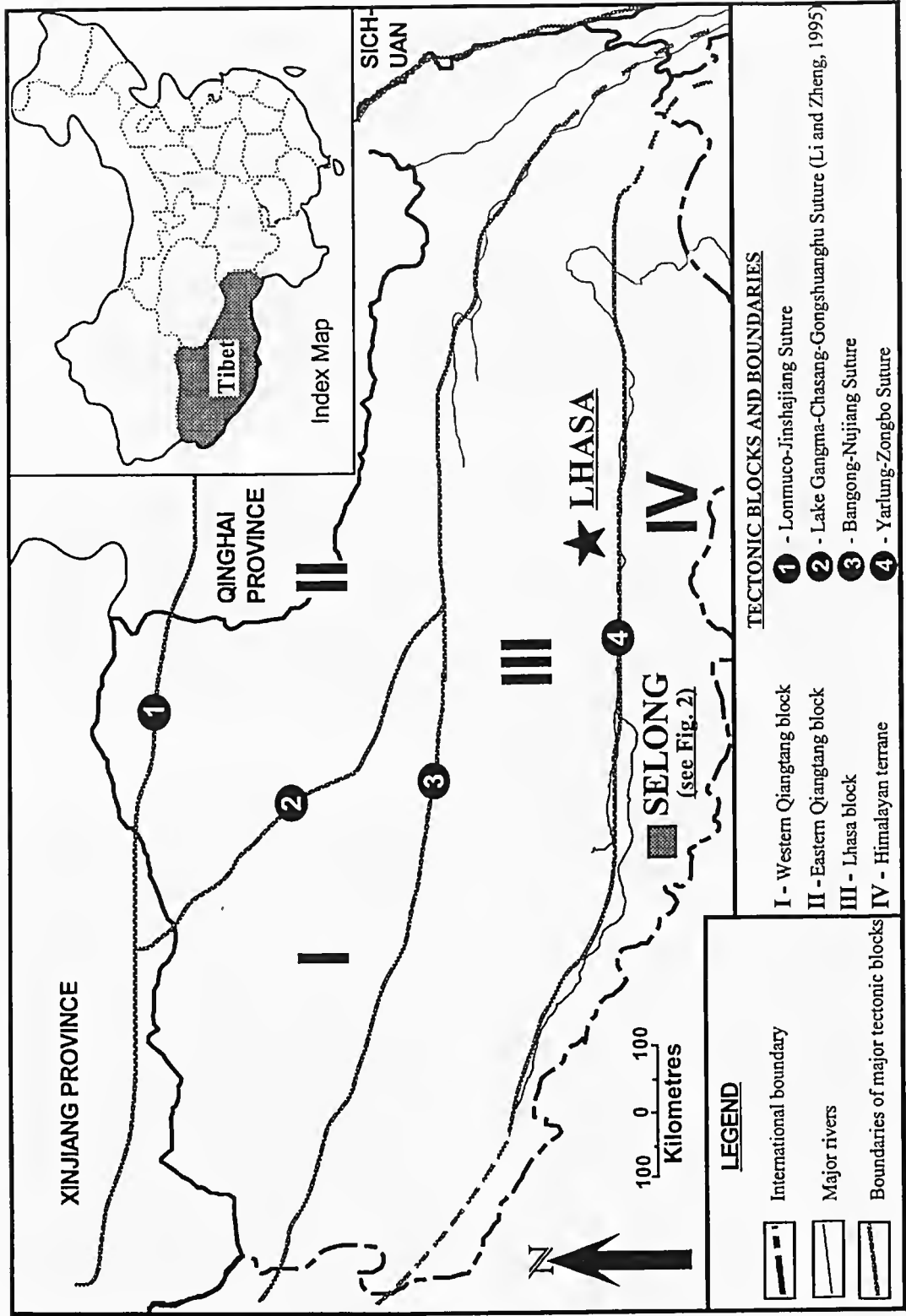


Fig. 1. Map showing major tectonostratigraphic blocks in Tibet and location of the study area.

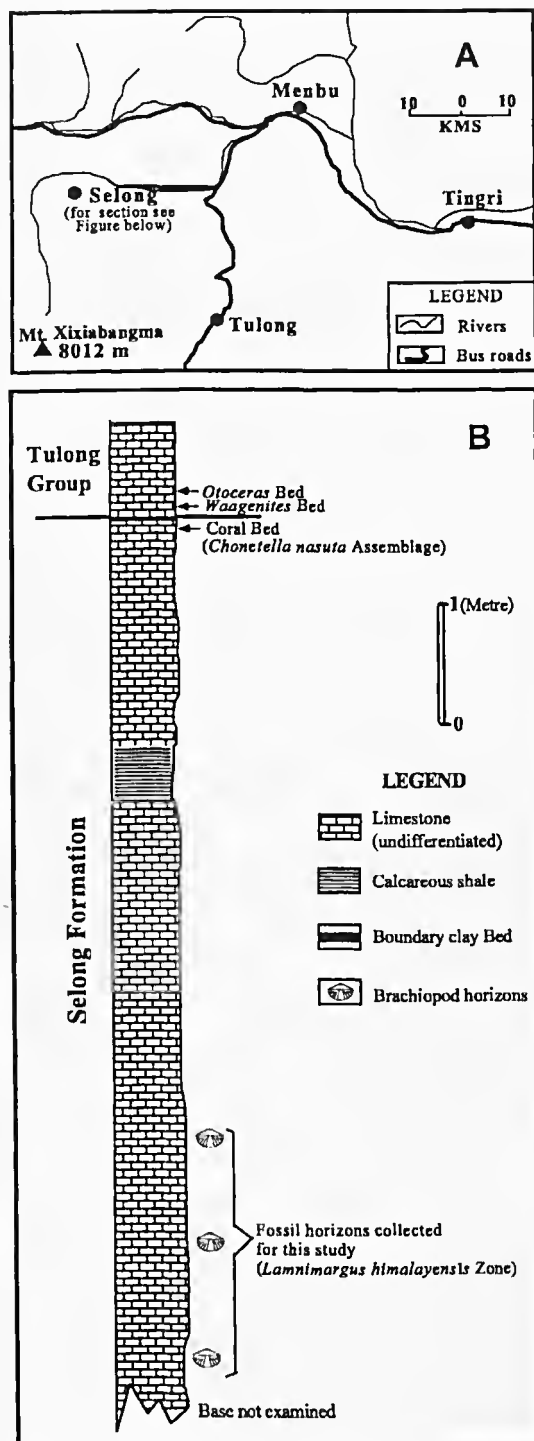


Fig. 2. A, detailed location map of Selong in southern Tibet. B, measured stratigraphic column of the Selong Formation at the Selong Xishan (Western Hills) section.

More recently, Wang et al. (1989), in an attempt to reveal the stratigraphical details of the supposedly continuous Permian–Triassic boundary at the Selong section, measured the section and divided the Selong Group into two parts; the lower part, named the 'Pre-Changhsingian Beds', was estimated to be 28.76 m thick and was characterised by grey to dark-grey limestones occasionally interbedded with calcareous shales. The upper part, called the 'Changhsingian Beds', was measured 0.06 to 0.17 m thick and was identified by grey and dark-grey limestone with a thin layer of clay and contained characteristic 'Changhsingian' conodonts and brachiopods. A further modification to the subdivision and nomenclature of the Selong Group in the Selong area has been proposed by Jin et al. (1996), who referred the carbonate-dominated Permian sequence to the Selong Formation, and the overlying dolomitic limestone facies to the Tulong Group, with the Permian–Triassic boundary being placed at the base of the 'Otoceras Bed' within the lower part of the Tulong Group (Fig. 2B). It is noted that in this scheme, which is also followed herein, the previously regarded uppermost calcareous shale-dominated unit (the so-called 'Waagenites Bed') of the Selong Group is now placed at the base of the Tulong Group (Fig. 2B).

The brachiopods described in this paper were collected from the middle part of the Selong Formation in the Selong section, from beds characterised by coarse bioclastic grainstones. The grains are dominated by poorly sorted broken brachiopod shells and crinoid stems; and the matrix is dominated by highly calcareous micrite and silt. The brachiopod specimens are abundant, but mostly fragmentary and disarticulated.

The fossils described in this paper are registered with the prefix NMV P and housed in the type collections of the Museum of Victoria, Melbourne.

AGE AND CORRELATION

In their study of Late Palaeozoic brachiopod faunas of Tibet, Zhang & Jin (1976) divided the brachiopod succession of the Selong Formation and equivalents in southern Tibet into two assemblages: the lower *Taeniothaerus* Assemblage characterising most of the Selong Formation, and the upper *Chonetella* Assemblage that occurs at the top of the formation. This latter fauna was later renamed the *Chonetella nasuta* Assemblage by Jin (1985). In a more recent study specifically on the brachiopods of the Selong section, Jin

et al. (1996) grouped the brachiopods of the Selong Formation from this section into a lower '*Marginifera*' (= *Lamnimargus*) *himalayensis*-*Spiriferella* Assemblage and an upper *Chonetella nasuta* Assemblage and restricted the latter assemblage to the top layer (their 'Coral Bed'; see Fig. 2B), just below the Permian-Triassic boundary 'Clay Bed'. The brachiopod material described in this report was collected from limestone beds about 5 m below the 'Coral Bed' and belongs to the '*Marginifera*' *himalayensis*-*Spiriferella* Assemblage (Fig. 2B).

In terms of species composition and stratigraphical position, the '*Marginifera*' *himalayensis*-*Spiriferella* Assemblage appears correlative with the *Lamnimargus himalayensis* Zone of Waterhouse (1976) and Waterhouse & Gupta (1977, 1983a). This zone, originally based on the Permian faunal sequence of Panjang Kola in the Dolpo district, northwest Nepal (Waterhouse 1976: 142, 143), was said to be typified by the brachiopod faunas of the lower Zewan beds (faunal Division I and II of Nakazawa et al. 1975) as originally described by Davidson (1862) and Diener (1899, 1915), with the following key species: *Neochonetes vishnu* (Salter), *Waagenoconcha gangeticus* (Diener), *Lamnimargus himalayensis* (Diener), *Costiferina alata* Waterhouse, *Anidanthus fusiformis* Waterhouse, *Spiriferella rajah* (Salter), *Neospirifer moosakhailensis* (Davidson), and *Fusispirifer nitiensis* (Diener) (Waterhouse & Gupta 1977). Two of these, *Lamnimargus himalayensis* and *Spiriferella rajah*, are also common in the Selong collection described herein, with a third species, *Neospirifer moosakhailensis*, being also closely comparable to *N. kubeiensis* Ting from the Selong assemblage. Several other diagnostic species of the *Lamnimargus himalayensis* Zone, though not recorded in this paper, have also been reported by Zhang & Jin (1976) from the Selong Formation near Selong and include *Costiferina alata* Waterhouse, *Anidanthus fusiformis* Waterhouse and *Fusispirifer nitiensis* (Diener).

The *Lamnimargus himalayensis* Zone appears to occur widely in the Himalayas, as reviewed by Waterhouse (1978) and Waterhouse & Gupta (1977), but only a few faunas have been systematically documented and many require modern revision. Important correlative faunal horizons include the Kalabagh Member of the Wargal Formation and, also possibly, the lower part of the Chhidru Formation of the Salt Range in Pakistan as described by Waagen (1882-1885) and Reed (1944) and discussed and reviewed by Grant (1970), the unnamed carbonate unit within the Shyok melange near Shigar, Baltistan, Pakistan

(Brookfield & Gupta 1984), the upper Kuling Group (formerly 'Kuling Shales') of Spiti, Lahaul and Zaskar (northwest India) (Garzanti et al. 1996), an unnamed metamorphosed silty shale unit in the upper Shoyok Valley in the Karakorum Range (Waterhouse & Gupta 1983b), the Lachi Group of North Sikkim (Muir-Wood & Oakley 1941), the unnamed micaceous shale beds of Kumaon and Garhwal (Diener 1897b, 1903), the '*Costiferina* arenites' unit of the Thini Chu Formation in northwest Nepal (Waterhouse 1966, 1978; Garzanti et al. 1992) and the 'Member C' of the Puchenpra Formation of central Nepal (Garzanti et al. 1994), and at least part of the Chitchun No. 1 Limestone of southern Tibet (Diener 1897a, 1903; Jin 1985).

The age of the *Lamnimargus himalayensis* Zone appears to be Midian-Early Dzhulfian, according to ammonoids and fusulinids found either in direct association with the brachiopods or immediately above the brachiopod horizon. In Kashmir, the basal two faunal divisions (Divisions I and II of Nakazawa et al. 1975) of the Zewan Formation, which provides the best reference section for the *Lamnimargus himalayensis* Zone (Waterhouse & Gupta 1977), is immediately overlain, without obvious hiatus, by faunal Division III, which contains a distinct *Cyclolobus* fauna of principally Dzhulfian age (see Glenister et al. 1990). The presence of *Cyclolobus*, overlying the *Lamnimargus himalayensis* Zone, therefore, sets an upper age limit for this brachiopod zone to be no younger than Dzhulfian. A similar stratigraphical relationship between *Cyclolobus* and the brachiopod zone has also been recorded within the Gungri Formation of the Kuling Group in Lingti of the Spiti Valley (northwest India), where *Cyclolobus walkeri* Diener of Dzhulfian age was found some 50 to 60 m above the *Lamnimargus himalayensis* Zone (Garzanti et al. 1996: 184).

The age of the *Lamnimargus himalayensis* Zone may be also inferred through its correlation with the Kalabagh Member of the Wargal Formation. Nakazawa & Kapoor (1979) have reported *Neoschwagerina* aff. *margaritae* from the lower Wargal Formation, *Colaniella nana* and *C. minima* (a key species of the Japanese Late Permian *Colaniella minima*-*Nanlingella simplex* Zone, of Dzhulfian age) and *C. pulchra* from the lower Chhidru Formation. These findings have confined the age of the Kalabagh and lower Chhidru Formation to the Midian-Dzhulfian range in terms of the Tethyan timescale (Leven 1992) or, by inference, the Capitanian-Wujiapingian in the framework of the newly proposed three-fold Permian timescale (Jin 1996).

SYSTEMATIC PALAEONTOLOGY

Order PRODUCTIDA

Sarycheva & Sokolskaya, 1959

Suborder STROPHALOSIIDINA

Waterhouse, 1975

Superfamily AULOSTEGACEA

Muir-Wood & Cooper, 1960

Family AULOSTEGIDAE

Muir-Wood & Cooper, 1960

Subfamily AULOSTEGINAE

Muir-Wood & Cooper, 1960

Genus *Taeniothaerus* Whitehouse, 1928*Type species. Productus subquadratus* Morris, 1845.*Taeniothaerus* sp.

Figs 3A–B

Taeniothaerus cf. *subquadratus* (Morris), Zhang & Jin 1976: 171, pl. 4, figs 1–3, 15–16.

Material and description. One incomplete ventral internal mould, NMV P145670, with part of the external mould of the ventral interarea attached. The valve is large, approximately 50 mm long and wide, 25 mm high, widest at midlength or near anterior margin, subquadrate in outline, strongly convex at midlength. Interarea approximately $\frac{2}{3}$ the maximum width, low, 8 mm high, concave, marked by very fine vertical striations, bisected by a narrow (1.5 mm) delthyrium, which is covered by strongly convex pseudodeltidium with a deep, V-shaped anterior notch about quarter the entire length of the pseudodeltidium. Sulcus prominent, commencing probably from umbo, broad and moderately deep towards anterior margin. Adductor scars relatively small and narrow, moderately raised, marked by few radial grooves; diductor scars large, lobate, strongly marked by elongate ridges, located mostly lateral to the adductor scars; rest of valve floor covered by slightly elongate pits, presumably reflecting external ornament. Several distinct concentric lamellae present at near anterior margin.

Comments. The present material is most like the specimens from the Selong Formation previously figured by Zhang & Jin (1976) as *Taeniothaerus* cf. *subquadratus* (Morris). The Selong species as a whole is characterised by a large size, subquadrate outline with a strongly curved lateral profile and maximum width being at or near the hinge line, and a well-defined ventral sulcus which is most pronounced over the mid-width of the shell. These characteristics suggest a strong similarity to *T. subquadratus* (Morris) from the Lower Artinskian Berricdale Limestone of Tasmania, as redescribed by Parfrey (1983). However, little is known about

the details of the ornament of the Selong species due to poor preservation, preventing a full comparison with the Tasmanian species. The overall shape and size of the Selong species also suggests *T. anotos* Briggs (in Waterhouse et al. 1983: 130, pl. 1, figs 6–10) from the Lower Artinskian of northern Bowen Basin, eastern Australia, but the latter appears to be more elongate in outline, with a shallow and broad sulcus. The well developed, strongly dendritic diductor scars of the Selong specimen also recalls *Megasteges* Waterhouse (1975), but the diductor scars of the latter are typically large and located lateral as well as anterior to the adductor scars.

Suborder PRODUCTIDINA Waagen, 1883

Superfamily PRODUCTACEA Gray, 1840

Family CHONETELLIDAE Likharev, 1960

Genus *Chonetella* Waagen, 1884*Type species. Chonetella nasuta* Waagen, 1884.*Chonetella nasuta* Waagen, 1884

Fig. 3C

Chonetella nasuta Waagen 1884: 613, pl. 81, figs 3–8.
Chonetella nasuta—Hamlet et al. 1928: pl. 3, figs 5–7
Chonetella nasuta—Muir-Wood & Cooper 1960: 219, pl. 69, figs 1–7.
Chonetella nasuta—Ternier et al. 1974: 129, pl. 28, figs 4–5.
Chonetella nasuta—Zhang & Jin 1976: 172, pl. 4, figs 4–5 (with synonymy).
Chonetella nasuta—Grant 1976: pl. 42, figs 1–17.
Chonetella nasuta—Jin 1985: pl. 4, figs 26–27.

Material and description. This distinctive species is represented by a ventral internal mould with broken patches of the exterior preserved. The specimen is small, about 10 mm wide (ears partly broken), 14 mm long, sub-ovate in shape, maximum width at hinge line; strongly and evenly convex without abrupt gcniculation, most convex at midlength; ears clearly defined, triangular in shape, slightly convex, well demarcated from strongly convex venter; umbonal slopes high and steep. Anterior margin notched to a narrow nasute extension, about 2 mm high and 3 mm wide. No reflection of external costellae observed on internal surface. Specimen too abraded to show details of muscle scars; no endospines or median septum.

Comparisons. Zhang & Jin (1976: pl. 4, figs 4–5) described and figured two ventral valves from the Selong Formation as *Chonetella nasuta*. A comparison of the combined characteristics of the present specimen and specimens figured by Zhang & Jin (1976) with the type material of *C. nasuta*

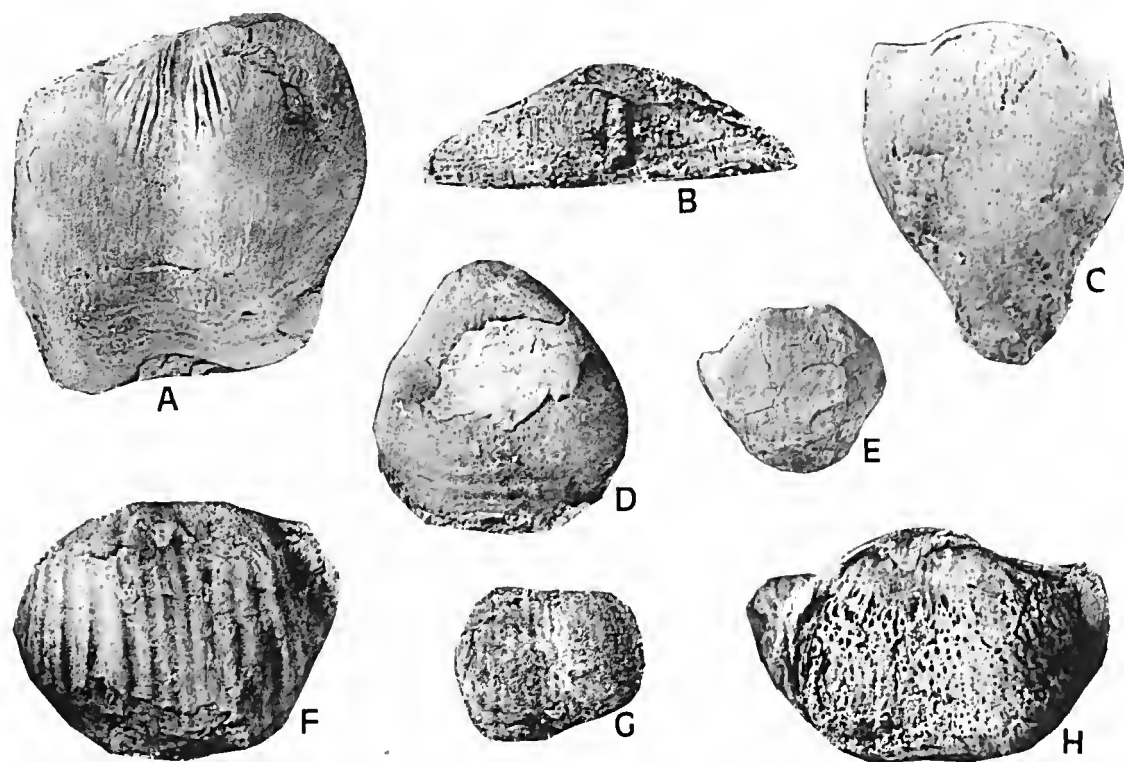


Fig. 3. A–B, a ventral internal mould and a latex cast of a ventral interarea of *Taeniothaerus* sp.; A, NMV P145670, $\times 1$; B, NMV P145671, $\times 1.5$. C, an abraded ventral valve of *Chonetella nasuta* (Waagen), NMV P145672, $\times 2$. D, a decorticated ventral valve of ?*Echinauris* sp., NMV P145673, $\times 2$. E, G, H, *Lamnimargus himalayensis* (Diener): E, an abraded ventral valve, NMV P145674, $\times 1$; G, latex cast of a ventral external mould, NMV P145676, $\times 1$; H, a ventral valve with interior partially exposed, NMV P145677, $\times 2$. F, ?*Lamnimargus* sp., a ventral valve, NMV P145675, $\times 2$.

as figured by Waagen (1884: 613, pl. 81, figs 3–8) and Grant (1976, pl. 4, figs 1–17) revealed strong similarities in all observed ventral details. Although no dorsal valves are available for the Selong form, the unique combination of its ventral characteristics, including a small size, strong and even convexity, moderate and well demarcated ears, weak to moderate costation, sparse spines restricted to along the hinge, and the presence of a distinctively notched anterior margin, serve to identify this form with *C. nasuta* and to distinguish it from other related species.

Likharev (1937: 12, pl. 13, figs 1–7) figured Upper Permian specimens from North Caucasia under the name of *Chonetella nasuta triangularis* var. nov. As the name implies, this species is characterised by a pair of large, laterally well extended ears; however, its median anterior notch is invariably small and short in comparison with that of *C. nasuta* from the Salt Range and Selong.

The same seems also true of the specimen figured as *Chonetella nasuta* Waagen by Hamlet (1928, pl. 3, fig. 8) from Wesleoe, West Timor, considered by Likharev (1937) to be conspecific with *C. triangularis*. However, Hamlet's other specimens (1928, pl. 3, figs 5–7), also from Wesleoe, possess a pair of smaller, though still very distinct, ears, much like in the present specimen and those of *C. nasuta* from the Salt Range, although the notched anterior margin of the Timorese specimens appears less well developed in comparison with most specimens of *C. nasuta* from the Salt Range. Rothpletz's (1892: 77, pl. 10, fig. 12) single ventral valve from Ajer Mati of West Timor appears to virtually lack the notched anterior margin characteristic of *C. nasuta*, as does a similar ventral exterior figured by Arehbold & Bird (1989: fig. 3A–B) from the Maubisse Formation near Kasliu, West Timor. It was noted by Arehbold & Bird (1989) that the lack of the anterior notch may

have been due to preservation, this nevertheless underlines a need for further study and clarification of the morphological range of material from Timor.

Waterhouse (in Waterhouse et al. 1981: 76, pl. 8, fig. 14) figured an externally abraded ventral valve from the Ko Yao Noi Formation of southern Thailand as *Chonetella* sp. This form resembles the Selong specimen in shape and size, but appears to be more inflated in profile.

Occurrences. *Chonetella nasuta* was originally described from the Kalabagh Member of the Salt Range in Pakistan. Elsewhere, the species has been recorded from the Amarassi and Basleo beds of Timor, the Selong Formation of southern Tibet, and from the Wardak area of central Afghanistan (see synonymy list).

Superfamily MARGINIFERACEA Stehli, 1954

(nom. transl. Shi & Waterhouse, 1996
ex Marginiferidae Stehli, 1954)

Family PAUCISPINIFERIDAE

Muir-Wood & Cooper, 1960

Subfamily RETIMARGINIFERINAE

Shi & Waterhouse, 1996

Genus *Lamnimargus* Waterhouse, 1975

Type species. *Marginifera himalayensis* Diener, 1899.

Comments. The genus has been discussed in some detail by Waterhouse (1975, 1978). When defining *Lamnimargus*, Waterhouse noted the close similarity of the genus with *Retimarginifera* Waterhouse (1970), type species *R. perforata* Waterhouse, from which Waterhouse recognised distinctions in shell structures, spine pattern on the ventral valve and the presence or absence of anterior flanges within both valves. However, the statement that *Lamnimargus* possesses a cluster of finer spines over each ear remains to be verified. Equally uncertain is the supposed presence of the anterior flanges (marginal ridges) thought by Waterhouse to characterise *Lamnimargus*, but Angiolini (in Garzanti et al. 1996) has pointed out that these marginal ridges are not present in the type specimens of Diener (1899).

Lamnimargus himalayensis (Diener, 1899)

Figs 3E, G, H

Marginifera himalayensis Diener 1899: 39, pl. 2, figs 1–7, pl. 4, figs 1–2.

Lamnimargus himalayensis—Gupta & Waterhouse 1979: 8, pl. 1, figs 3–8 (with synonymy).

Lamnimargus himalayensis—Brookfield & Gupta: 1984: 41, fig. 7.

Lamnimargus himalayensis—Waterhouse & Gupta 1983b: 237, pl. 1, fig. 10, pl. 3, fig. 5.

'*Lamnimargus*' *himalayensis*—Angiolini in Garzanti et al. 1996: 194, pl. 1, figs 1–2.

Description This species is represented by three ventral valves, NMV P145674, P145676 and P145677, including a fragmentary ventral external mould. The specimens are small, 25 mm wide and about 22 mm long, transverse in outline, widest along hinge line; moderately convex; ears relatively large, lobate in shape, well demarcated from umbonal slopes; visceral disc moderately convex, sharply geniculated anteriorly into trail; sulcus prominent, commencing about 4 mm from umbo, deepest over middle valve. Ventral ornament consists of well defined costae and concentric rugae, the latter being confined to visceral disc area; reticulation pattern poorly preserved due to abrasion; costae generally uniform in strength, low but clearly recognisable, 8 to 9 per 10 mm at midlength, no bifurcation or intercalation observed, no sign of convergence in sulcus. Ventral spines poorly preserved, but one pair of strut spine bases are seen, one on each flank near sulcus.

Ventral adductor and diductor scars partially observed, weakly striated; valve floor anterior to the muscle scars covered by close-set, well-differentiated endospines, becoming finer towards marginal ridge, no endospines on interior of trail; marginal ridge weak, no anterior flanges observed.

Comments. The present specimens are poorly preserved; however, their shape, size and characteristics of the ears, the low but well-defined costae and details of the sulcus suggest a close similarity to *Lamnimargus himalayensis* Diener (1899) from the lower Zewan Formation of Kashmir. The Selong specimens are generally smaller than the syntypes figured by Diener, but this seems to be a variable feature. For instance, Gupta & Waterhouse (1979) also figured a small, reticulate ventral valve as *Lamnimargus himalayensis*. This is also true of the specimens figured as the same species by Zhang & Jin (1976, pl. 10, figs 17–21).

Occurrences. *Lamnimargus himalayensis* seems to have a restricted stratigraphical and geographical distribution. As discussed earlier, this species is the key form of the *Lamnimargus himalayensis* Zone which is widely distributed in the Himalayan region. It has been recorded from Pakistan, Bhutan, Nepal, southern Tibet, Kashmir, northwest India, Sikkim and Karakorum. The occurrences of the species from Cambodia as recorded by Chi-Thuan

(1961, pl. 1, figs 12–14; 1962, pl. 2, fig. 4) and from Beishan of northern Gansu Province, north-west China (Ustritskiy 1963, pl. 5, fig. 3) require verification; these specimens are characterised by finer, more closely set and more prominent costellae. Specimens figured as *Probolionia himalayensis* (Diener) by Grunt (in Grunt & Dmitriev 1973, pl. 5, figs 13, 14) are small, but with relatively large transverse ears and a more transverse visceral disc. Personal inspection by GRS of the Pamirian species at the Palaeontological Institute of the Russian Academy of Sciences in August 1995 revealed a very narrow visceral cavity and a deep and relatively narrow sulcus, suggesting either *Uraloproductus* Ustritskiy or *Retimarginifera* Waterhouse. Archbold (1984: 115) had previously assigned the Pamirian material to *Retimarginifera*.

?*Lamnimargus* sp.

Fig. 3F

Comments. A poorly preserved ventral valve NMV P145675 in the Selong collection seems to suggest a different species closely related to *Lamnimargus* or an allied genus, but with clear difference from the species described above. The ventral valve is compatible in size, shape, sulcus to *Lamnimargus himalayensis* Diener but characterised by distinctively high, coarse costellae numbering 5 to 6 per 10 mm at midlength; some of the costellae tend to bifurcate near the anterior margin.

Family COSTISPINIFERIDAE Muir-Wood & Cooper, 1960

Genus *Echinauris* Muir-Wood & Cooper, 1960

Type species. *Echinauris lateralis* Muir-Wood and Cooper, 1960.

?*Echinauris* sp.

Fig. 3D

Echinauris opuntia (Waagen), Zhang & Jin 1976: 173, pl. 7, fig. 9.

Comments. A possible species of *Echinauris* is indicated by a ventral valve NMV P145673 in the Selong material. The specimen is measured 32 mm wide and 34 mm long, subcircular to slightly elongate in outline, strongly convex without distinct geniculation, no sulcus; umbo strongly incurved over hinge; visceral disc strongly convex with high and steep umbonal slopes; ears not

preserved, maximum width possibly located at midlength. The only preserved patch of ventral exterior shows presence of very fine spine bases, about 1 to 1.5 mm in diameter, possibly quincuncially arranged, no costellae or concentric rugae are observed on the preserved patch of the ventral exterior although a pair of concentric lamellae are imprinted on the internal mould near the anterior margin.

Ventral muscle scars located on posterior third to quarter of valve floor; adductor scars on low, narrow median platform, possibly smooth; diductor scars weakly depressed, smooth or weakly striated. Numerous fine pustules or granules present anterior to muscle scars, about 1 mm in diameter.

This single specimen is possibly conspecific with *Echinauris opuntia* (Waagen 1884: 707, pl. 79; figs 1–2; Grant 1976: 27, pl. 8, figs 1–8; pl. 9, figs 1–8) from the Kalabagh Member of the Wargal Formation of the Salt Range, Pakistan, in terms of the observed details of the ventral valve in hand. However, detailed comparison is hampered by the lack of sufficient material, especially the absence of dorsal details. The Selong specimen shares with the Pakistani species a subquadrate outline, a strongly incurved ventral umbo and fine, numerous spines over the venter. However, because of the lack of dorsal details the possibility of this specimen belonging to other closely related Costispiniferidae genera, such as *Costispinifera* Muir-Wood and Cooper, cannot be ruled out.

A poorly preserved ventral valve figured as *Echinauris opuntia* by Zhang & Jin (1976: 173, pl. 7, fig. 9) from the Selong Formation of Tingri is considered conspecific; it shares all the observable features with those of the present specimen.

Order ATHYRIDIDA Dagys, 1974

Superfamily ATHYRIDACEA McCoy, 1844

Family ATHYRIDIDAE McCoy, 1844

Genus *Cleiothyridina* Buckman, 1906

Type species. *Atrypa pectinifera* Sowerby, 1840.

Cleiothyridina sp.

Fig. 4A.

Comments. One dorsal valve NMV P145688 with part of a ventral posterior attached is indicative of the presence of *Cleiothyridina* in the Selong assemblage. The dorsal valve is about 3 cm wide and 2.5 cm long, subcircular in shape; gently

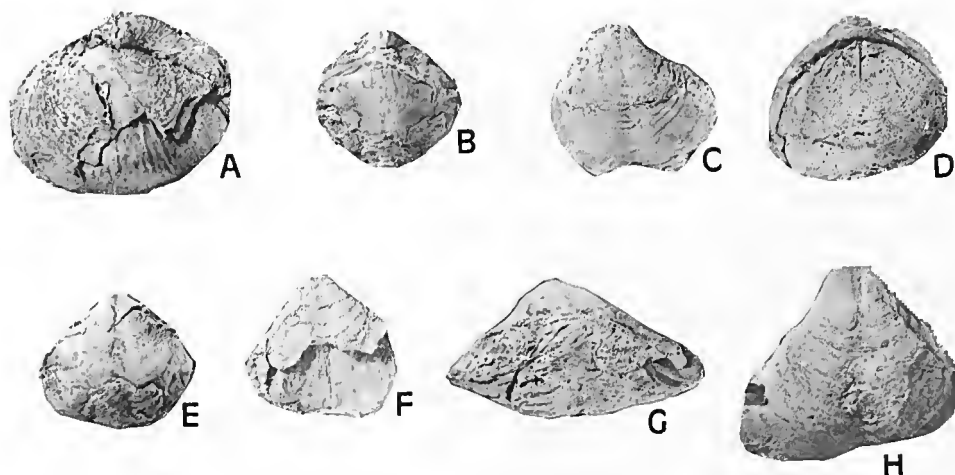


Fig. 4. A, *Cleiothyridina* sp., dorsal valve with part of ventral valve attached, NMV P145688, $\times 1$. B-H, *Posicomta grunti* n. sp.: B, E, G, holotype, dorsal, ventral and anterior views of an articulated shell, NMV P145689, B, E, $\times 1$; G, $\times 1.5$; C, ventral valve, NMV P145693, $\times 1$; D, dorsal view (showing the internal mould) of an articulated shell, NMV P145691, $\times 1.5$; F, ventral view (showing part of the exposed ventral internal mould) of an articulated shell, NMV P145690, $\times 1$; H, ventral valve, NMV P145692, $\times 2$.

to moderately and evenly convex, with no conspicuous fold. Fine, close-set concentric lamellae prominent, about 2 per 1 mm near anterior margin; the anterior edge of each laminae 'saw-teeth' fringed, indicating the attachment of fine spines along the edge of the lamellae. Dorsal interior marked by distinct radial vascular markings, which tend to subdivide towards anterior margin.

This single specimen is most likely to be conspecific with specimens attributed to *Cleiothyridina royssii* (Eveillé) from the Wargal and Chhidru Formations of the Salt Range (Davidson 1862: 27, pl. 1, fig. 6; Waagen 1883: 475, pl. 39, fig. 10; pl. 30, figs 6-12) in terms of shell size, convexity and shape. *C. capillata* (Waagen 1883: 479, pl. 39, figs 6-9; pl. 40, figs 1-5; pl. 42, figs 1-5; Grant 1970: 141, pl. 2, figs 16-17) from the upper Chhidru Formation is also close in shell size and outline, but is readily distinguishable from the present specimen by its high convexity.

Family SPIRIGERELLIDAE Grunt, 1965

Genus *Posicomta* Grunt, 1986

Type species. *Posicomta gundarensis* Grunt, 1986.

Diagnosis (Grunt 1986: 120). Shell small, length about equal to width; subpentagonal in outline, moderately biconvex, both valves with equal con-

vexity; sulcus weak, fold normally absent but a furrow or fine groove may be present along the median symmetry plane of some dorsal valves. Umbo low, moderately incurved; foramen small to moderately large, rounded. Delthyrium broad, triangular in shape, completely concealed by dorsal umbo. Shell surface normally smooth or with weak concentric growth lines only along the anterior margins of shell.

Ventral interior with teeth and short, divergent dental plates; teeth small, pointing inwards. Dorsal interior with inner and outer hinge plates and a weak median septum; inner hinge plates depressed below outer hinge plates; median septum usually small, never connecting to hinge plates. Ventral muscle impressions weak, lobate in shape. Shell strongly thickened; shell structure consists of two layers, primary layer made of fine, prismatic calcite micro-crystals and second layer fibrous; fibres large.

Discussion. This genus is closest to *Composita* Brown and *Tulathyris* Grunt, from the former it may be distinguished by its small size and thick shell, and from *Tulathyris* it differs by its thick shell. *Spirigerella* Waagen also shares some general morphological characteristics with *Posicomta* but is distinguished in having its greatest width typically placed anterior to midlength, a short, usually strongly incurved beak with no or a small foramen, and ill-defined dental plates.

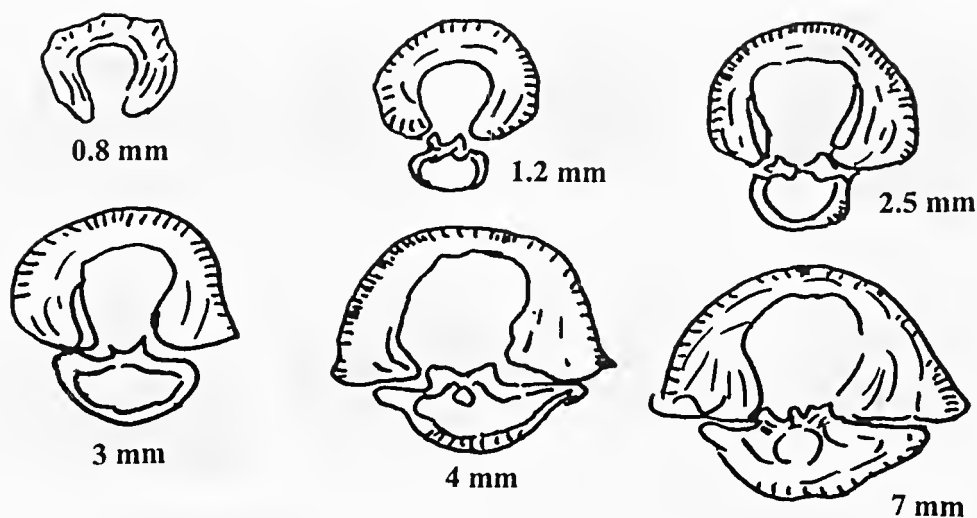


Fig. 5. Serial sections of *Posicomta grunti* n. sp. Numbers adjacent to the figures indicate distances in mm from umbo, all $\times 3$.

Posicomta grunti n. sp.

Figs 4B–H, 5

Etymology. In honour of Dr T. A. Grunt, a respected colleague and teacher, who also examined this species while visiting Australia in December 1996.

Material. Four articulated shells NMV P145688–P145691 and one ventral valve NMV P145692.

Holotype. NMV P145689, an articulated shell figured in Figs 4B, E, G.

Diagnosis. Shell medium to large, subovate in shape, both valves equally convex; median groove prominent on ventral valve, variable on dorsal valve; anterior commissure uniplicate. Dental plates ill-defined, mostly buried within posterior shell wall. Dorsal interior with a prominent median septum.

Description. Shell medium to large, 1.5 to 3.5 cm wide, 1.6 to 2.5 cm long, and 0.8–1.3 cm thick, subovate in outline with maximum width at midlength; both valves moderately to strongly and equally convex, with greatest convexity at midlength; umbo narrow with umbonal slopes converging posteriorly at about 15–20°, umbonal slopes gently to moderately concave in profile, high and steep; beak elongated, moderately incurved; foramen relatively small, mostly obscured by matrix; delthyrium totally concealed by dorsal beak. No obvious sulcus or fold except at anterior margin the commissure is clearly uniplicate in the

holotype (Fig. 4G); a prominent median groove present in all ventral valves, commencing from beak and extending and broadening towards anterior margin; no prominent corresponding median groove seen on dorsal valve.

Shell surface smooth except for a few broadly spaced concentric growth lines or lamellae concentrated on anterior two thirds of shell; posterior third of shell smooth.

Specimen NMV P145692 was sectioned to reveal internal structures (Fig. 5). No clear, isolated dental plates found within posterior 2 mm from umbo, but a pair of thin, darkened ridges observed from a thin section at about 2.5 mm from umbo, still attached to the shell wall; the darkened colour can be clearly distinguished from the white, prismatic microcrystals of calcite that make up the second layer of the shell structure. In holotype, a pair, almost parallel, of darkened ridges were also observed from the umbonal area (at about 1–2 mm from beak) under microscope. Hinge plates subquadrate in shape, medially concave. Dorsal median septum prominent, extending for 5–8 mm from beak. Ventral muscle field only partially observable in specimen NMV P145690 (Fig. 5F), lobate and relatively large, occupying about posterior third of valve floor, slightly depressed; moderately striated; vascular markings present, prominent around muscle field, weaker towards lateral and anterior margin.

Shell structure of two distinct layers; primary layer of fine, prismatic (perpendicular to shell

surface) calcite crystals; second layer (outer layer) of microscopic calcite fibres parallel or at low angle to shell surface.

Comparison. The new species is particularly close to the type species *Posicomta gundarensis* Grunt (1986: 120, pl. 16, figs 9–11; fig. 63) from the Kubergandian Gundaren Formation of southwest Darvas in the Pamir Range. The two species share a similar size, suboval shape and, in particular, a prominent median groove on the ventral valve and a variably developed median groove on the dorsal valve. However, the new species shows a more elongated and attenuated umbo and beak, resulting in more concave umbonal slopes. A comparison of the thin sections of the new species with those of *P. gundarensis* also reveal some significant internal differences. The dental plates in the type species are separated from the thickened shell material almost from the beak, whereas they appear to be buried in the shell material for almost their entire length in the new species. No dorsal median septum seems to have been revealed in the sectioned specimen of *P. gundarensis* although the genus was diagnosed as having a weak dorsal median septum. This is in contrast to a prominent median septum in the dorsal interior of the new species.

Four other species have also been assigned to *Posicomta*. *P. zaalaica* Grunt (Grunt 1986: 122, p. 16, figs 12, 13) from the Kubergandian beds of the Trans-Alaica Range in Turkestan is a small species lacking median grooves on both valves. Three species described by Grant (1976) as *Composita* from the Rat Buri Limestone of southern Thailand have been transferred to *Posicomta* by Grunt (1986). *P. advena* (Grant 1976: 205, pl. 56, figs 1–60) and *P. dolabrata* (Grant 1976: 206, pl. 57, figs 21–31) are both smaller than *P. grunti*, with a conspicuous triangular shape due to its elongated and posteriorly narrowed and pointed umbonal region. *P. subsolana* (Grant 1976: 209, pl. 57, figs 1–17) is the largest of the three Thai species, approaching the largest specimen of the new species; it also has a well developed dorsal median septum, resembling the new species. However, the anterior commissure of the Thai species is more strongly uniplicate, some even sulcificate. The Thai species also lacks the characteristic median grooves of *Posicomta grunti*.

Order SPIRIFERIDA Waagen, 1883

Superfamily SPIRIFERACEA King, 1846

Family SPIRIFERELLIDAE Waterhouse, 1968

Genus *Spiriferella* Chernyshev, 1902

Type species. Spirifer saranae Verneuil, 1845

Comments. The familial status of *Spiriferella* and allied genera is still of debate (Carter 1974; Archbold & Thomas 1985; Angiolini 1995). Termier & Termier (in Termier et al. 1974) recognised the distinctiveness of the spiriferid group and proposed Spiriferellidae as a new family, apparently unaware of the earlier proposal by Waterhouse (1968). Shi & Waterhouse (1996), in accepting Termier & Termier's proposal, have also recognised the validity of the family Spiriferellidae. This family now includes 7 genera in addition to *Spiriferella*: *Elivina* Fredericks, *Eridmatus* Branson, *Alispiriferella* Waterhouse & Waddington, *Plicatospiriferella* Waterhouse & Waddington, *Timaniella* Barchatova, *Rhombospirifer* Duan & Li and *Huizina* Angiolini. A possible additional genus, *Tintoriella* Angiolini (in Garzanti et al. 1996), may be also included (see Discussion below).

Distinction of *Spiriferella* from *Elivina*, *Eridmatus*, *Alispiriferella*, *Plicatospiriferella*, *Timaniella* and *Rhombospirifer* have been discussed in some detail by Waterhouse et al. (1978), Waterhouse & Waddington (1982), Archbold & Thomas (1985) and Shi & Waterhouse (1996). *Huizina* was considered by Angiolini (1995: 187) to differ from *Spiriferella* by its 'open delthyrium, lower dorsal fold, less fasciculated ornamentation, shorter dental plates which are strongly embedded in the apical callus'. However, the practicality of using the presence or absence of a pseudodeltidium as one of the key diagnostic characteristics in distinguishing Spiriferellinae genera needs to be cautioned because the lack of a pseudodeltidium which may be originally present may well be due to preservation. This is evident, for instance, from the illustration of *Spiriferella gravis* Cooper & Grant (1976: 2230, pl. 630, figs 1–40) from the Word Formation of west Texas of the United States. Most of their figured ventral vales (eg. pl. 630, figs 17, 29, 31, 33) clearly show the presence of a convex pseudodeltidium over the delthyrium, but others (eg. pl. 630, figs 27, 39) show no sign of such a structure, which has presumably been broken.

Tintoriella Angiolini (in Garzanti et al. 1996) was based on large specimens of *Spiriferella rajah* (Salter) from the northwest Himalayas and was distinguished from *Spiriferella* by means of 'the open delthyrium, longer dental plates and adminicula which are not embedded in the apical callus' (Angiolini in Garzanti et al. 1996: 195). However,

as described below, a well preserved ventral internal mould of what is believed to be *Spiriferella rajah* from the Selong Formation does not exhibit the isolated adminicula as observed by Angiolini. In this specimen, almost the entire adminicula seem to be buried within the secondary shell thickening below the delthyrium. This may imply that the contact relationship between the adminicula and the posterior shell wall is a variable feature, presumably reflecting ontogenetic changes and/or environmental control. In some specimens, for instance the ventral interior of *Spiriferella rajah* figured by Diener (1915, pl. 9, fig. 6), the adminicula are apically buried within the shell wall but anteriorly become separated. The same seems also true with '*Tintoriella*' *rajah*, judging from its serial sections figured by Angiolini (in Garzanti et al. 1996, pl. 1, figs 8–13). In this sectioned specimen, the adminicula do not become separated from the apical callus until about 5.5 mm from the beak. The variable feature of the adminicula in relation to the apical callus in *Spiriferella* and allies has also been demonstrated by Waterhouse & Waddington (1982) from a large collection of specimens from western and northern Canada (eg. *Spiriferella saranae* sectioned by Waterhouse & Waddington 1982, fig. 14).

On the other hand, the Selong ventral valve (Fig. 6A) does show an open delthyrium and a pair of thickened, subparallel dental plates, but it cannot be ascertained from the specimen whether or not the delthyrium was originally open or closed by a pseudodeltidium. For the above reasons, *Spiriferella* is retained for Salter's species.

Spiriferella rajah (Salter, 1865)

Figs 6A–I

Spirifer rajah Salter in Salter & Blanford 1865: 59, 111, 2 figs in p. 59.

Spirifer rajah—Davidson 1866: p. 40, pl. 2, fig. 3.

Spirifer rajah—Diener 1899: 68, pl. 4, figs 1–7; pl. 5, fig. 1.

Spirifer rajah—Diener 1903: 105, 131, 186, pl. 4, figs 3–5.

Spiriferella rajah—Waterhouse 1966: 48, pl. 1, fig. 5; pl. 3, fig. 2; pl. 7, figs 1, 2, 4; pl. 11, fig. 2; pl. 12, fig. 2.

Spiriferella rajah—Muir-Wood & Oakley 1941: 36, pl. 2, figs 2, 3, 9–11.

Spiriferella rajah—Zhang & Jin 1976: 215, pl. 17, figs 3–12.

Spiriferella rajah—Waterhouse in Gupta & Waterhouse 1979: 11, pl. 1, figs 10–14; pl. 2, figs 1–10; pl. 3, fig. 1.

Spiriferella rajah—Waterhouse & Gupta 1983b: 238, pl. 2, figs 1–2.

Spiriferella rajah—Brookfield & Gupta: 1984, figs 5, 6, 8.

Spiriferella rajah—Garzanti et al. 1992: 280.

Spiriferella rajah—Garzanti et al. 1994: pl. 1, fig. 5.

Tintoriella rajah—Angiolini in Garzanti et al. 1996: 195, pl. 1, figs 6–13.

Diagnosis. Large, subquadrate to slightly elongate *Spiriferella*; shell maximum width normally at hinge or slightly anterior to it; ventral umbo massive, strongly incurved; dorsal fold lacking median groove; plieae prominent, low, well rounded, separated by narrow interspaces, strongly costate, each plicae consisting of up to 7 costae.

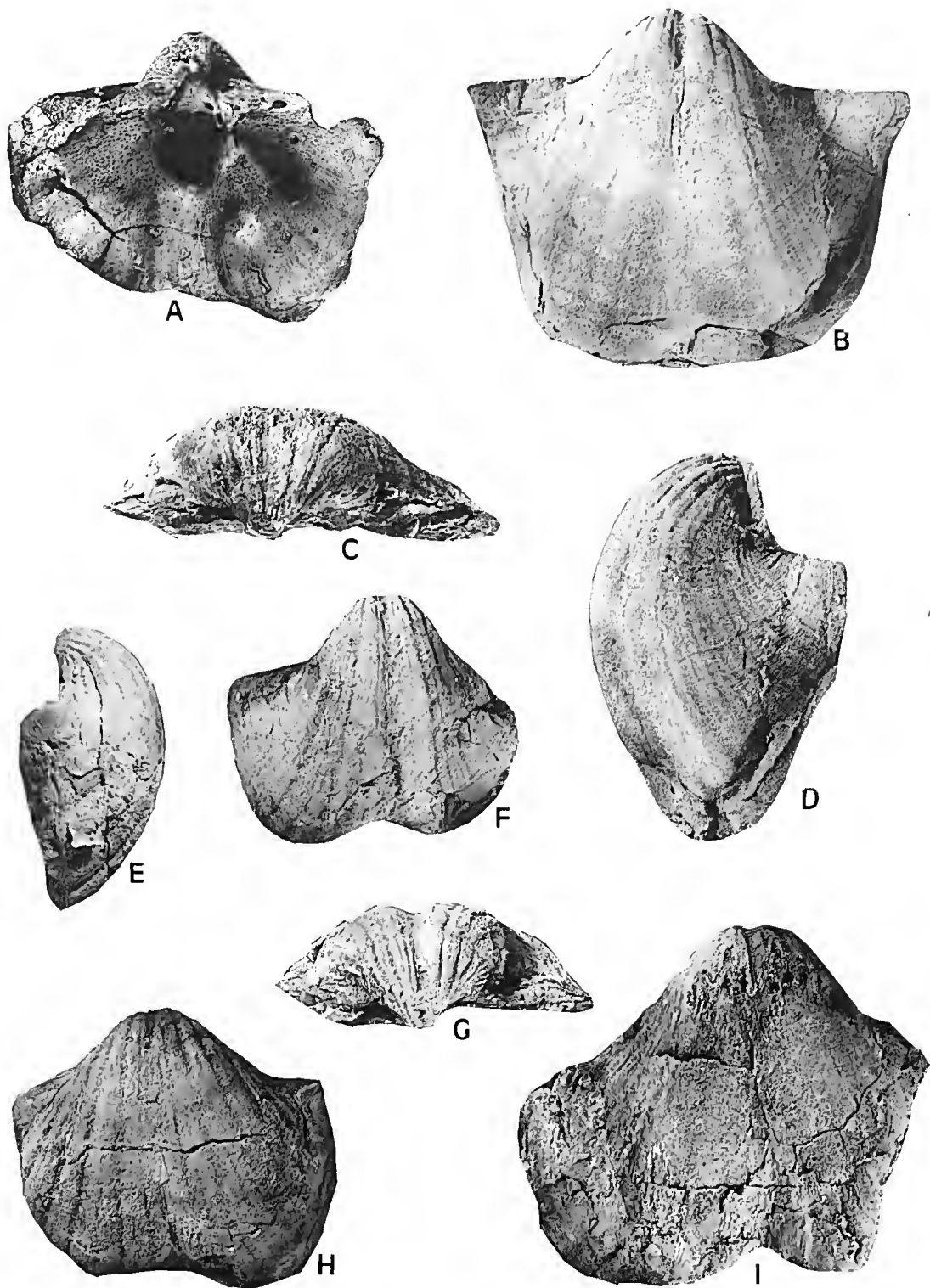
Material. Seven ventral valves and one ventral internal mould, of which five are figured herein, NMV P145678–P145682.

Description. Shell large, maximum width 68 mm, length more than 55 mm; subquadrate in outline, widest at hinge line or slightly anterior to it. Interarea relatively small, high, triangular in shape, moderately concave, weakly marked by striations; delthyrium relatively large; pseudodeltidium unknown.

Ventral valve strongly and evenly convex, maximum convexity at midlength; umbo massive, strongly incurved with beak hanging over delthyrium; umbonal slopes high and steep, straight or gently inflated in outline, diverging anteriorly at about 65° to 70°; ears large, well extended laterally, triangular in shape, flattened in profile, clearly segregated from venter by angle close to 80–90°. Suleus prominent, commencing from umbo, widening forwards at about 20°, moderately deep, clearly defined by first pair of plieae, sulcal floor V-shaped in section, floor angle (measured at anterior margin) varying from 110° to 114°. Lateral flanks rounded in cross section with relatively high and steep slopes.

Five to six pairs of plieae observed on all ventral valves, commencing from umbo where they are clearly separated from each other by interspaces equal to or slightly narrower than plieae; anteriorly,

Fig. 6. *Spiriferella rajah* (Salter). A, ventral valve, NMV P145678. B, D, ventral and lateral views of a ventral valve, NMV P145679. C, I, posterior and ventral views of a ventral valve, NMV P145680. E, G, H, lateral, posterior and ventral views of a ventral valve, NMV P145681. F, ventral valve, NMV P145682. All in natural size.



plicae tend to be lower, more flattened, well rounded in section, and less clearly demarcated from each other due to fasciculation; first bifurcation of plicae occurs at about 10 to 15 mm from beak; secondary costation appears at about midlength; in some specimens, particularly larger ones (Figs 6B, D), further branching of plicae seems evident at near anterior margin resulting in equi- or nearly equidimensional costate appearance in some specimens; up to three pairs of costae observed in sulcus, with no prominent median costa.

Micro-ornament is preserved on parts of one ventral valve (NMV P145679, Fig. 6D), consisting of relatively well defined lamellae, crossed by very fine radial capillae; lamellae numbering 2 to 3 per mm and capillae 3 to 4 per mm on ears; fine, low pustules arise from capillae, often at intersections with concentric lamellae, numbering 2 to 3 per mm.

Umbonal area of ventral interior strongly thickened, resulting in a thick apical callus just below posterior part of delthyrium; teeth robust, probably also thickened, supported by prominent dental plates, which, along with low adminicula, are posteriorly buried by apical callus; muscle field relatively short, posteriorly placed below delthyrium, clearly delineated from the rest of valve floor by raised, posteriorly thickened surrounding ridges, oval or diamond in shape, deeply depressed posteriorly and raised in front where it then passes into a narrow, high supporting ridge, anteriorly striated; muscle field bisected by a fine median ridge commencing from apical callus; adductor and diductor scars poorly differentiated; areas surrounding the muscle field covered by vascular markings.

Comparisons. The diagnosis of *Spiriferella rajah* given above is based on the illustrations and descriptions of the species provided by Salter (in Salter & Blanford 1865) and Davidson (1866) in conjunction with observations made from the present material. A comparison of Salter's original drawings of *S. rajah* with those of Davidson reveals two discrepancies, presumably a reflection of artistic interpretation or intraspecific variations. The specimen illustrated by Salter shows that the maximum width of the species is at hinge line and the dorsal fold is as strongly costate as plicae on lateral flanks. These two features are in contrast with the relatively short hinge (shorter than the maximum width) and a largely smooth or weakly costate fold depicted for the same species by Davidson.

The Selong specimens at hand can be closely

compared with *Spiriferella rajah* of Salter in shell shape, a wide hinge that represents the maximum width of the shell, a massive and strongly incurved umbo, and costate sulcus and fold. The two illustrations of *S. rajah* given by Salter are smaller than the largest specimens described here (NMV P145679) but are well compatible with the other ventral valves such as NMV P145678, NMV P145681–P145682.

The species has been previously recorded from many localities, only some of which are considered to be truly conspecific with the type material based on the diagnosis given above for the species (see synonymy list). Other forms that have also been recorded under the same species name but whose morphological features are inconsistent with the diagnosis herein provided have been excluded from the synonymy, as discussed below. *Spiriferella rajah* is readily distinguished from most other species of *Spiriferella* by its large size, subquadrate outline, wide hinge normally marking the maximum width of the shell, a massive, strongly incurved umbo, and low, broad, well-rounded and strongly costate plicae. Some of these features are shared with several large *Spiriferella* found in the Kazanian–Midian beds of northeast Asia and Australia. Fredericks (1916) recognised six varieties/forms (or subspecies) of *Spiriferella rajah* from the lower Upper Permian of the Russian Far East. Identity of these forms with true *Spiriferella rajah* has been questioned by Li (in Ding et al. 1985), who grouped and reclassified them into two species: *Spiriferella magna* Fredericks and *S. saranaeformis* Fredericks. The former, which also occurs in the Permian Zhesi Formation of Inner Mongolia, is a large subquadrate to subrounded *Spiriferella*; it differs from *S. rajah* by its narrow hinge line and a broad and deep sulcus. *S. saranaeformis* is comparable with *S. rajah* in size but has an elongate outline coupled with a high and strongly incurved interarea (rather like typical *S. saranae*). Grabau (1931) also assigned several large specimens from the Zhesi Formation respectively to *Spiriferella salteri* (Chernyshev) and *S. keilhavii* (von Buch). These Inner Mongolian specimens resemble *S. rajah* in size and the broad hinge line that marks the shell maximum width, but they both have high and weakly costate plicae, in contrast to the low, broad and strongly costate plicae of *S. rajah*.

Spiriferella grandis Kotlyar (in Likharev & Kotlyar 1978: 73, pl. 18, figs 7–8) from the Midian Chandalaz Formation of the Russian Far East is very close to the Selong material in shell size and shape, but seems to have a broader and deeper sulcus and more prominent plicae separated by

deeper interspaces. Archbold (1995) also figured a large, subquadrate *Spiriferella* from a deep drilling core of the northern Perth Basin of Western Australia, believed to be of Ufimian age; however, this Australian species has a relatively narrower hinge and its maximum width is near the anterior margin.

Occurrences. As implied by the synonymy list of *Spiriferella rajah* shown above, this species is widely distributed in the Himalayan region where it has been recorded from northern Pakistan, Nepal, southern Tibet, Kashmir, northwest India, and Sikkim. The species appears to be restricted to the *Lannimargus himalayensis* Zone of Midian–Early Dzhulfian age.

Family SPIRIFERIDAE King, 1846

Subfamily NEOSPIRIFERINAE Waterhouse, 1968

Genus *Neospirifer* Fredericks, 1924

Type species. *Spirifer fasciger* von Keyserling, 1846.

Neospirifer kubeiensis Ting, 1962

(emend. Chang emend. nov. 1976)

Figs 7B–D

Neospirifer moosakhailensis Ting 1962: 452, pl. 1, figs 1–6.

Neospirifer kubeiensis Ting 1962: 453, pl. 2, figs 1–3.

Neospirifer tibetensis Ting 1962: 454, pl. 2, figs 4, 5.

Neospirifer kubeiensis—Zhang & Jin: 1976, 203, pl. 14, figs 1–4, 8–9; pl. 15, figs 1, 2; pl. 16, fig. 8; pl. 19, fig. 2; figs 10, 11).

Neospirifer kubeiensis—Waterhouse 1978: 125, pl. 24, figs 4–7.

Neospirifer tibetensis—Yang & Zhang 1982: 312, pl. 3, figs. 2–4; fig. 1.

Neospirifer kubeiensis—Yang et al. in Yang & Nie 1991: pl. 25, fig. 9.

Neospirifer kubeiensis—Fang & Fan 1994: pl. 31, figs 10–12; pl. 32, figs 1, 2 (see also Fang 1995: 140, pl. 5, figs 10–12; pl. 6, figs 1, 2).

Description. This large *Neospirifer* species is represented by three ventral valves, one of which is nearly complete. The shell is moderately transverse, 94 mm wide and 60 mm long; subtrigonal in shape; gently and evenly convex in profile. Umbo moderately incurved with umbonal angle close to 110°; umbonal slopes low, broadly rounded in cross section, gently concave in profile. Interarea low (about 14 mm high), broadly triangular in shape; delthyrium concealed by sediment. Hinge line wide, equal to or slightly narrower than the

maximum width of shell; cardinal extremities blunt with cardinal angle about 90°. Sulcus very pronounced, commencing from umbo, 5 mm wide at 10 cm from umbo and increasing to about 40 mm wide near anterior margin; sulcal floor broadly rounded, sulcal height close to 10 cm, deepest at anterior margin.

Shell ornament consisting of three pairs of prominent plicae on lateral flanks, one pair of plicae on sulcal slopes, equidimensional costae on both flanks and in sulcus, and a well-defined median costa within sulcus. Plicae broad, relatively low and rounded in crest, decreasing in strength towards cardinal extremities so that areas of flanks near cardinal extremities are nonplicate but covered by fine costae; plicae asymmetrical in cross-section with its broader and more gentle slope oriented towards sulcus; each plica consisting of a bunch of up to 6 equidimensional costae each about 1.4 mm across. Pair of plicae on sulcal slopes much weaker than those on flanks, most pronounced over posterior third of sulcus where they define the initial edges of sulcus from flanks, becoming progressively weaker anteriorly until they are completely and evenly dispersed as costae within the sulcus. Costae within the sulcus equidimensional, each about 1.4 mm across, about 15 on each sulcal slope; median sulcal costa distinct, slightly coarser than other sulcal costae, persisting from umbo to anterior margin.

Comments and comparisons. Ting (1962) recognised three large *Neospirifer* species from the upper Permian of southern Tibet: *N. moosakhailensis* (Davidson), *N. kubeiensis* Ting and *N. tibetensis* Ting, based on the relative size of shell, number of plicae on flanks and costae within sulcus, and the width of hinge with respect to shell maximum width. Zhang & Jin (1976) examined some 45 specimens representative of all the three species from southern and central Tibet and observed that the criteria used by Ting were features of considerable variation, which they believed to be primarily related to ontogenetic changes. As a consequence, Zhang & Jin broadened the definition of *N. kubeiensis* as originally outlined by Ting to accommodate a wide range of variation and included *N. tibetensis* as a junior subjective synonym of *T. kubeiensis*.

As also noted by Zhang & Ching (1976), *N. kubeiensis* is very close to *N. moosakhailensis* (Davidson 1862, pl. 2, fig. 2) from the Wargal and Chhidru Formations of the Salt Range, agreeing in size, shape, and plication and costation patterns, but the Pakistani species, the lectotype of which was refigured by Waterhouse (1978, pl. 26,

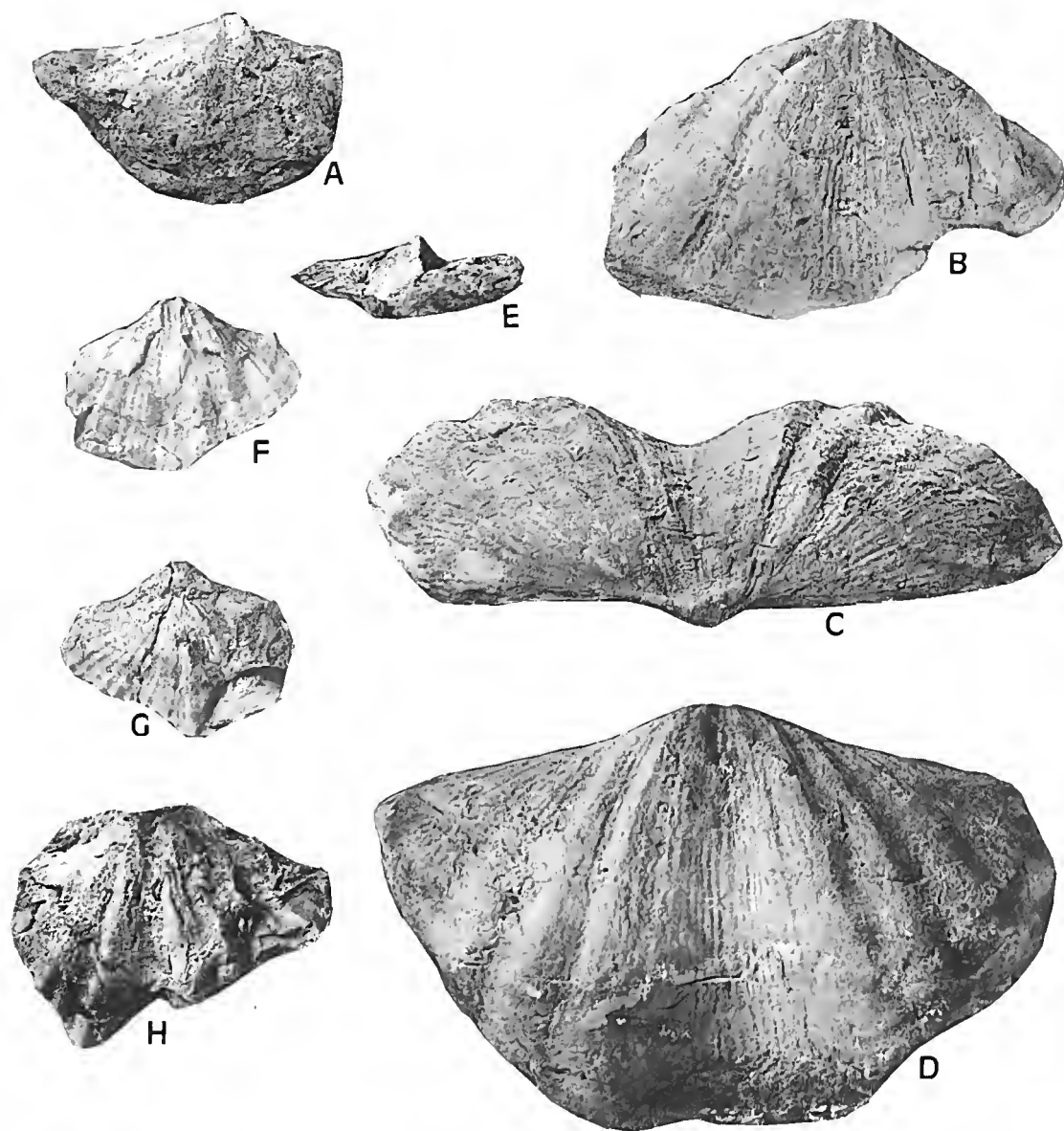


Fig. 7. A, E-G, *Trigonotreta* sp.: A, ventral valve, NMV P145683, ×1; E-G, anterior, ventral and dorsal views of articulated shell, NMV P145684, ×1. B-D, *Neospirifer kubeiensis* (Ting): B, ventral valve, NMV P145687, ×1; C-D, posterior and ventral views of ventral valve, NMV P145685, ×1. H, Spiriferinacean gen. et. sp. indet., ventral valve, NMV P145686, ×2.

figs 4-7), lacks a pair of subplicae within the sulcus that otherwise characterises *N. kubeiensis*.

The moderately transverse outline, strong and distinct lateral plications, a broad and deep sulcus with a pair of weak sulcal plicae of *N. kubeiensis*

suggest similarities to a group of large to moderately large *Neospirifer* species from the Sakmarian-Artinskian beds of Western Australia (Archbold & Thomas 1986), including *Neospirifer foordi* Archbold and Thomas, *N. plicatus* Archbold

and Thomas and *N. postplicatus* Archbold and Thomas. The first of these species possesses a sharp, angular-floored sulcus lacking lateral plicae and its costae appear to be finer than those of the present material. The other two Western Australian species are closer to *N. kubeiensis* in many respects, particularly in terms of shell size, shape, strong plications, and sulcal plicae, but they both have attenuated cardinal extremities at maturity. *N. postplicatus* is further distinguished from *N. kubeiensis* in lacking the third pair of lateral plicae on flanks, which is prominent in *N. kubeiensis*.

Occurrences. *Neospirifer kubeiensis* has been recorded from the Wargal and Chhidru Formations of the Salt Range, Pakistan, the upper Kuling Group or equivalent beds in northwest Himalayas, the Selong Formation or equivalents in central and southern Tibet, and the Dadongchang Formation of western Yunnan, China.

Subfamily TRIGONOTRETINAE Schuchert, 1893

Genus *Trigonotreta* Koenig, 1825

Type species. Trigonotreta stokesii Koenig 1825.

Trigonotreta sp.

Figs 7A, E-G

Comments. The presence of *Trigonotreta* within the Selong collection is indicated by a decorticated ventral valve (NMV P145683) and an articulated shell (NMV P145684). Although there are only limited features observable, the Selong material, especially specimen NMV P145684 (Fig. 7E-G), does show the characteristic fascicles of *Trigonotreta*, with three costae derived from a primary plica. Specimen NMV P145683 also shows the typical trigonal shape of *Trigonotreta*, while specimen NMV P145684 is comparatively more transverse. The latter specimen also exhibits closely spaced concentric lamellae, 3-4 per mm, and a prominent median costa within the sulcus. The fold of specimen NMV P145684 is relatively narrow, high and sharp-crested. The inadequate preservation of the Selong form does not warrant any closer comparisons with described species.

Order SPIRIFERINIDA Cooper & Grant, 1976

Suborder SPIRIFERINIDINA Ivanova, 1972

Superfamily SPIRIFERINACEA Davidson, 1884

Spiriferinacean gen. et. sp. indet.

Fig. 7H

Comments. An incomplete, decorticated ventral valve with coarse, simple costae and a smooth sulcus probably indicates a Spiriferinacean genus in the Selong assemblage. The valve is more than 2 cm wide and more than 1.5 cm long, moderately convex. Sulcus prominent, relatively deep with sulcal floor broadly U-shaped, no costellae present within sulcus; at least four pairs of costae present on lateral flanks, simple and extending from umbo to anterior margin; relatively high and well rounded in section. No microornament is observable on the decorticated surface.

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GASTROPODA, SCAPHOPODA, CEPHALOPODA AND NEW BIVALVIA OF THE PALEOCENE PEBBLE POINT FORMATION, VICTORIA, AUSTRALIA

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DARRAGH, THOMAS A., 1997:11:30. Gastropoda, Scaphopoda, Cephalopoda and new Bivalvia of the Paleocene Pebble Point Formation, Victoria, Australia. *Proceedings of the Royal Society of Victoria* 109 (t): 57-108. ISSN 0035-9211.

The molluscan fauna of the Paleocene Pebble Point Formation, Otway Basin, Victoria, Australia, contains forty-six gastropods of which 21 are formally described; three scaphopods, of which two are new; two cephalopods; and thirty-seven bivalves, of which six are newly described. New species are *Rimula crepiduloides*, *Puncturella* (*Altrix*) *caminata*, *Calliotropis microglyptophorus*, *Bathymophila bystromphalata*, *Conominolia parvistrigulata*, *Cirsochilus pilulatus*, *Colposigma uniangularata*, *Euspira saxosulensis*, *Austrofusus*? *crassiaulatus*, *Levifusus quadrifunifer*, *Columbarium rugatoides*, *Mitra*? *rhytidata*, *Proximitra trirugulata*, *Zemacies procerior*, *Marshallaria tumefacta*, *Cosmasyrinx* (*Tholotoma*) *levicristata*, *Acteon petricolus*, *Tornatellaea quindecimlirata*, *Gilbertina meridiana*, *Priscaphander bullariformis*, *Spiratella advenulata*, *Compressidens laticornuata*, *Gadila laguncula*, *Austronucula*? *arenaria*, *Comitileda brachyrhynchoides*, *Electroma glessaria*, *Linea* (*Notolimea*) *multicostulifera*, *Jagolucina psephenata*, *Bornia flabellaris*, *Cuspidaria obbata*. *Superstes glomerabilis* is described from the Early Eocene Dilwyn Formation. The fauna has no close affinity with any other, consisting in the main of cosmopolitan genera. Endemic genera are *Botelloides* and *Eotrigonia*. Genera with a Southern Hemisphere affinity are the bivalves, *Lahillia*, *Neilo* (*Australoneilo*), and gastropods, *Colposigma*, *Marshallaria* and *Zemacies*.

Keywords: Gastropoda, Scaphopoda, Cephalopoda, Bivalvia, Late Paleocene, Otway Basin, Victoria, Australia, palaeoecology, biogeography, taxonomy, new taxa.

PALEOCENE MOLLUSCA occur in the Pebble Point Formation of the Otway Basin, Victoria, Australia (Baker 1943, 1950). The major portion of the bivalve fauna and the general features of the formation were described by Darragh (1994). The remainder of the molluscan fauna is described here and also some new bivalve species. The previous paper recorded 32 bivalve taxa. Here five extra taxa are recorded making a total of 37 bivalves. There are 46 gastropods, three scaphopods and two cephalopods. Of the gastropods, three are represented by such poor material that meaningful comparisons are not possible. Twenty-one gastropods are formally described and the others recorded in open nomenclature because there is insufficient material to permit formal naming.

One scaphopod, *Fissidentalium gracilicostatum*, was described by Singleton (1943), the other two are new. The two cephalopods, *Aturoidea distans* and *Eutrephoceras victorianum*, were described by Teichert (1943, 1947).

The material described here was collected from the Pebble Point Formation outcrops along the coast southeast of Princetown, Victoria. A few specimens are included from inland localities near Hamilton (Spencer-Jones 1971) and Casterton (Kenley 1951, 1971).

PEBBLE POINT FORMATION MOLLUSCAN FAUNA

For convenience a complete checklist of the molluscs is given here.

Gastropoda

Fissurellidae

Emarginula sp.

Rimula crepiduloides sp. nov.

Puncturella (*Altrix*) *caminata* sp. nov.

Cocculinidae

Cocculina? sp.

Trochidae

Calliotropis microglyptophorus sp. nov.

Bathymophila bystromphalata sp. nov.

Conominolia parvistrigulata sp. nov.

Botelloides sp.

Turbinidae

Guildfordia (*Opella*)? sp.

Turbinidae gen. et spec. indet.

Cirsochilus pilulatus sp. nov.

Pareuchelus sp.

Turritellidae

Colposigma uniangularata sp. nov.

Turritellidae gen. et spec. indet.

- Naticidae
 Euspira saxosulensis sp. nov.
 Naticid sp. a
 Naticid sp. b
 Ranellidae
 Sassia sp.
 Epitoniidae
 Opalia (Pliciscula?) sp.
 Epitoniidae gen. et sp. indet.
 Buccinidae
 Austrofuscus crassiaulatus sp. nov.
 Pseudofax cf. ordinarius (Marshall)
 Levifusus quadrifunifer sp. nov.
 Fasciolaridae
 Fusinus sp.
 Turbinellidae
 Columbarium rugatoides sp. nov.
 Microfulgur? sp.
 Mitridae
 Mitra? rhytidata sp. nov.
 Volutomitridae
 Proximitra trirugulata sp. nov.
 Olividae
 Pseudoliva (Buccinorbis) sp.
 Turridae
 Zemacies procerior sp. nov.
 Cosmasyrinx (Tholotoma) levicristata sp. nov.
 Marshallaria tumefacta sp. nov.
 Marshallaria sp. a
 Marshallaria sp. b
 Acteonidae
 Acteon petricolus sp. nov.
 Acteon sp. b
 Tenuiactaeon sp.
 Tornatellaea quindecimlirata sp. nov.
 Ringiculidae
 Gilbertina meridiana sp. nov.
 Cylichnidae
 Cylichnania sp.
 Priscaphander bullariformis sp. nov.
 Mathildidae
 Tuba sp.
 Pyramidellidae
 Odostomia sp.
 Amathinidae
 Raulinia sp.
 Limicinidae
 Spiratella advenulata sp. nov.
 Incertae sedis
 gastropod with canal
 Scaphopoda
 Dentaliidae
 Dentalium (Fissidentalium) gracilicostatum
 Singleton
 Compressidens laticornuata sp. nov.
 Gadilidae
 Gadila laguncula sp. nov.
 Cephalopoda
 Nautilidae
 Eutrephoceras victorianum (Teichert)
 Hercoglossidae
 Aturoidea distans Teichert
 Bivalvia
 Nuculidae
 Lamellinucula pyrenoides Darragh
 Nucula
 Austronucula? arenaria sp. nov.
 Nuculanidae
 Comitileda brachyrhynchoides sp. nov.
 Ledina paucigradata Singleton
 Neilo (Australoneilo) cultrata Darragh
 Cucullacidae
 Cucullaea psepheia Singleton
 Limopsidae
 Limopsis rupestris Darragh
 Glycymeridae
 Glycymeris sp.
 Pinnidae
 Pinna sp.
 Pteriidae
 Electroma glessaria sp. nov.
 Propeamussiidae
 Parvamussium sp.
 Pectinidae
 Delectopecten sp.
 Anomiidae
 Anomia sp.
 Limidae
 Limea (Notolimea) multicostulifera sp. nov.
 Gryphaeidae
 Pycnodonte (Phygraea) sp.
 Trigoniidae
 Eotrigonia paleocenica Darragh
 Lucinidae
 Jagolucina psephenata sp. nov.
 Lucinid A
 Lucinid B
 Myrtea faseolata Darragh
 Thyasiridae
 Thyasira sp.
 Ungulinidae
 Felaniella (Zemysia) sp.
 Erycinidae
 Bornia flabellaris sp. nov.
 Cyamiidae
 Cyamiocardium silicula Darragh
 Astartidae
 Astarte (A.) notialis Darragh
 Carditidae
 Venericardia (Rotundicardia) petraea Darragh
 Carditellopsis bellissima Darragh

Lahilliidae
Lahillia australica Singleton
 Tellinidae
Bertinella lapidaria Darragh
 Corbiculidae
Corbicula?
 Veneridae
Dosinia (Dosinobia) saxatilis Darragh
Callistina (Tikia)? scopulensis Darragh
 Corbulidae
Caryocorbula sp.
 Hiatellidae
Panopea sp.
 Cuspidariidae
Cuspidaria obbata sp. nov.
 Verticordiidae
Verticordia sp.

PALAEOECOLOGY

Trophic composition

The reservations about the validity of a trophic analysis of the bivalve fauna expressed by Darragh (1994) apply equally well here and are not repeated. Broad general groupings of the gastropods, scaphopods and cephalopods according to feeding type are as follow:

Grazers. *Emarginula* sp., *Rimula crepidinoides* sp. nov., *Puncturella (Altrix) caminata* sp. nov., *Calliotropis microglyptophorus* sp. nov., *Bathymophila bystromphalata* sp. nov., *Conominolia parvistrigulata* sp. nov., *Botelloides* sp., *Guildfordia (Opella)?* sp., Turbinid, *Cirsochilus pilulatus* sp. nov., *Pareuchelus* sp.

Deposit, suspension feeders. *Colposigma uniangulata* sp. nov., Turritellid, *Spiratella advenulata* sp. nov.

Carnivores. *Euspira saxosulensis* sp. nov., Naticid sp. a, Naticid sp. b, *Sassia* sp., *Austrofusus crassiusculus* sp. nov., *Pseudofax cf. ordinarius* (Marshall), *Levifusus quadrifunifer* sp. nov., *Fusus* sp., *Columbarium rugatoides* sp. nov., *Microfulgur?* sp., *Mitra? rhytidata* sp. nov., *Proximitra trirugulata* sp. nov., *Pseudoliva (Buccinorbis)* sp., *Zemacies procerior* sp. nov., *Cosmasyrinx (Tholotoma) levicristata* sp. nov., *Marshallaria tumefacta* sp. nov., *Marshallaria* sp. a, *Marshallaria* sp. b, *Acteon petricolus* sp. nov., *Acteon* sp. b, *Tenuiactaeon* sp., *Tornatellaea quindecimlirata* sp. nov., *Gilbertina meridiana* sp. nov., *Cyliclomania* sp., *Priscaphander bullariformis* sp. nov.

Symbiotic carnivores. *Opalia (Pliciscala?)* sp., Epitoniid.

Parasites. *Odostomia* sp., *Raulinia* sp., *Tuba* sp.

Pelagic predatory carnivores. *Eutrophoceras victoriauum* (Teichert), *Aturoidea distans* Teichert.

On comparing the above groupings with the table of numbers of specimens studied, it will be seen that the three species of gastropods forming 45% of the specimens collected fall into two groups. Two of these species, *Cirsochilus pilulatus* and *Conominolia parvistrigulata* which form 33% of the specimens collected, are assumed to be grazers and the other, *Colposigma uniangulata*, a presumed deposit feeder or suspension feeder, comprises 12%. Carnivores make up the largest group of species, as distinct from specimens, as might be expected. Of these, opisthobranchs comprise 23% of all specimens collected. Naticids are the only carnivores which have left a trace of their activities. It is assumed that they are responsible for the holes drilled in the bivalves (Darragh 1994).

Unlike the bivalves, it has not been possible to find relevant gastropods in communities in Recent seas, except that *Turritella* is a characteristic member of some of the Recent Northern Hemisphere cool shallow water communities (Thorson 1957).

A taxonomic structure analysis of the fauna was undertaken using the criteria set out in Maxwell (1992) and the results compared with the standard profiles established by Hickman (1984) using percentages of major mollusc groups for palaeobathymetric interpretation. This technique is based on the assumption that the proportions for shelf, bathyal and abyssal depths have remained constant through time.

Table comparing percentages of major molluscan groups in modern faunas with those from the Pebble Point Formation (PPt)

	Shelf	Bathyal	Abyssal	PPt	PPt*
Gastropoda					
Archaeogastropoda	8	20	21	26	26
Mesogastropoda	34	23	21	17	20
Neogastropoda	41	52	41	30	30
Opisthobranchia	18	6	18	25	22
<i>Incertae sedis</i>				2	2
*pyramidellids included with Mesogastropoda					
Bivalves					
Protobranchs	6	28	40	16	
Pteromorphs	19	21	20	27	
Heterodonts	70	22	15	49	
Septibranchs	5	28	20	8	

The profile of the Pebble Point gastropod fauna does not resemble any of the Hickman profiles. In particular, the percentage of opisthobranchs is very high, even when the pyramidellids are included with the mesogastropods which was probably the case in Hickman's analysis. The Pebble Point gastropod profile comes closest to the Abyssal profile, which is at variance with the other evidence. The bivalve profile is closest to that of the shelf, which is in accordance with other evidence. Assuming that the Hickman profiles hold good for the southern hemisphere and for faunas of the earliest Tertiary, the discrepancy in the gastropod profile may possibly be explained by the extremely shallow nature of the Pebble Point Formation. Also the fauna is relatively small, about 83 species, with many species represented by only one specimen, so that the finding of even one specimen each of additional species has a considerable effect on the percentages.

ENVIRONMENT AND DEPOSITION

The Gastropoda and Cephalopoda add a little to what has been stated previously, viz. that the Pebble Point Formation was deposited in a shallow-water, open ocean environment (McGowran 1965; Darragh 1994). The presence of the pelagic gastropod *Spiratella* in reasonable numbers as well as two species of cephalopods suggest that the Pebble Point Formation was deposited in an open ocean environment. One worn and poorly preserved turbinid gastropod may have been living on a hard bottom and transported some distance before burial. There are no other undoubted hard bottom dwellers present. As with the bivalves, many of the gastropods show considerable abrasion, suggesting transport before burial. Other specimens are well preserved or delicate, such as *Spiratella*, which seems to indicate that they were buried without being transported in sediment to any significant extent.

BIOGEOGRAPHY

In the previous paper on the bivalves (Darragh 1994), I expressed caution concerning biogeographic analysis because of the uncertainties of the generic placement of some of the taxa, both in the Pebble Point fauna and in Paleocene faunas around the world. The same remarks apply equally, if not more so, to the gastropods.

Table showing numbers of specimens used in this study.

Gastropods	
<i>Cirsochilus pilulatus</i> sp. nov.	266
<i>Colposigma uniangulata</i> sp. nov.	140
<i>Conominolia parvistrigulata</i> sp. nov.	112
<i>Gilbertina meridiana</i> sp. nov.	94
<i>Priscaphander bullariformis</i> sp. nov.	85
<i>Austrofusius crassiusculus</i> sp. nov.	60
<i>Tornatellaea quindecimlirata</i> sp. nov.	59
<i>Spiratella advenulata</i> sp. nov.	36
<i>Marshallaria tumefacta</i> sp. nov.	33
<i>Euspira saxosulensis</i> sp. nov.	32
<i>Calliotropis microglyptophorus</i> sp. nov.	24
<i>Bathynophila</i> ? <i>bystromphalata</i> sp. nov.	23
Naticid sp. a	22
<i>Rimula crepiduloides</i> sp. nov.	21
<i>Proximitra trirugulata</i> sp. nov.	20
<i>Mitra</i> ? <i>rhytidata</i> sp. nov.	16
<i>Cosmasyrinx</i> (<i>Tholotoma</i>) <i>levicristata</i> sp. nov.	13
<i>Fusinus</i> sp.	11
<i>Cyclchnania</i>	11
<i>Odostomia</i>	10
<i>Puncturella</i> (<i>Altrix</i>) <i>caminata</i> sp. nov.	9
<i>Acteon petricolus</i> sp. nov.	6
<i>Levisus quadrifunifer</i> sp. nov.	6
<i>Zemacies procerior</i> sp. nov.	6
<i>Columbarium rugatoides</i> sp. nov.	4
<i>Botelloides</i>	4
<i>Acteon</i> sp. b	3
gastropod sp.	3
Epitoniid	2
<i>Pseudofax</i> cf. <i>ordinarius</i>	2
<i>Pseudoliva</i> (<i>Buccinorbis</i>) sp.	2
<i>Marshallaria</i> sp. b	2
<i>Opalia</i> (<i>Placiscala</i> ?) sp.	2
<i>Marshallaria</i> sp. a	2
<i>Microfulgur</i> ?	1
<i>Pareuchelus</i>	1
<i>Guildfordia</i> (<i>Opella</i>) ?	1
Naticid sp. b	1
<i>Sassia</i> sp.	1
<i>Tuba</i> sp.	1
Turritellid	1
Turbinid	1
<i>Tenuitactaeon</i> sp.	1
<i>Cocculina</i> ? sp.	1
<i>Emarginula</i>	1
<i>Raulinia</i>	1
Total	1153
Scaphopoda	
<i>Dentalium</i> (<i>Fissidentalium</i>) <i>gracilicostatum</i>	64
<i>Compressidens laticornuata</i> sp. nov.	61
<i>Gadila laguncula</i> sp. nov.	10
Total	135
Cephalopoda	
<i>Eutrepoceras victorianum</i>	9
<i>Aturoidea distans</i>	15
Total	24

Four Paleocene faunal groupings were outlined by Darragh (1994).

1. Early Paleocene Boreal fauna.
2. Temperate to warm temperate fauna of Southern Europe and America.
3. Tropical Tethyan fauna.
4. Southern Hemisphere fauna.

Group four is not a homogeneous grouping when compared with the other three.

The new records of bivalves reported here include *Nucula*, *Glycymeris*, *Delectopecten*, *Bornia* (previously recorded as *Borniola*?) and *Corbicula*? which are all cosmopolitan genera in cool to warm temperate faunas. One subgenus, *Linea* (*Notolinea*), is known living off the east coast of Australia and from the Tertiary of Australia, New Zealand and Europe. The bivalves, therefore, are overwhelming cosmopolitan in aspect, though with little affinity to group 3.

The three scaphopod genera, *Fissidentalium*, *Compressidens* and *Gadila*, are all cosmopolitan in distribution, though in the case of *Compressidens*, the genus has not previously been recorded earlier than Miocene.

The two cephalopod genera, *Eutrephoceras* and *Aturoidea*, are cosmopolitan in the Paleocene.

Of the 46 gastropods, only 13 seem to be related to taxa found in the New Zealand Paleocene: *Conominolia*, *Guildfordia* (*Opella*)?, *Colposigma*, *Euspira*, *Pseudofax*, *Microfulgur*?, *Zemacies*, *Marshallaria*, *Cosmasyrinx* (*Tholotoma*), *Acteon*, *Tornatellaea*, *Cyllichnania*, *Priscaphander* and *Tuba* (Marshall 1917; Finlay & Marwick 1937). Of these *Conominolia*, *Euspira*, *Pseudofax*, *Acteon*, *Tornatellaea* and *Tuba* are considered to be cosmopolitan genera and *Guildfordia* (*Opella*) (known from the New Zealand Miocene) and *Microfulgur* are recorded from the Pebble Point Formation with considerable doubt. These occurrences do not suggest a particularly strong relationship with New Zealand Paleocene faunas (Marshall 1917; Finlay & Marwick 1937; Beu & Maxwell 1990).

The genera in common with the Antarctic Late Eocene are *Colposigma*, *Pseudofax*, *Zemacies*, *Acteon*, *Tornatellaea* and *Tuba* (Stilwell & Zinsmeister 1992), of which the latter three and *Pseudofax* are cosmopolitan in distribution.

Puncturella (*Altrix*), *Levifusus* and *Tenuiactaeon* were previously known only from southeastern North America. *Rimula* and *Pareuchelus* are representatives of the European elements of Group two.

The only undoubted Australian endemic genus recorded is *Botelloides*.

The Pebble Point Formation gastropods are thus dominated by cosmopolitan genera and show no particular faunal affinity with any other Paleocene fauna, a feature also shown by the bivalve fauna. Unlike the bivalve fauna, which had two 'southern hemisphere' endemics present, *Lahillia* and *Neilo* (*Australoneilo*), there are no such elements present in the gastropod fauna, unless *Colposigma*, *Marshallaria* and *Zemacies* be considered such. The typical Austral elements, the struthiolariids, are entirely lacking and do not make an appearance in the Australian fauna until the Early Miocene (Darragh 1991). A truly Australian endemic presence is also very weak. This element is only represented by the taxa, *Eotrigonia* and *Botelloides*. As with the bivalves, the gastropods indicate that an endemic Australian fauna was not established in shallow water in the Paleocene. Such a fauna was established by the Late Eocene, at which time New Zealand and Tethyan/Indo-Pacific immigrants were also present, all forming the basis of the modern Southern Australian molluscan fauna.

The conclusions about the molluscan fauna existing in the seaway opening up between Australia and Antarctica (Frakes et al. 1987; Veevers et al. 1991) based on the study of the bivalves are thus reinforced by the evidence of the gastropods. Cosmopolitan taxa with presumed pelagic larvae established themselves first as shown by the Pebble Point Formation fauna and by early Eocene time an endemic element had evolved in the fauna and immigrants from the New Zealand and Tethyan regions became established (Darragh 1985).

RELATIONSHIPS WITH OLDER AUSTRALIAN FAUNAS

The next oldest fauna known in Australia is that found in the Maastrichtian Miria Formation of Western Australia (Darragh & Kendrick 1994). None of the gastropods of this formation are related to those in the Pebble Point Formation, with the possible exception of the taxon recorded as *Fusinus*?

RELATIONSHIPS WITH YOUNGER FAUNAS

Though species of *Fissidentalium*, *Emarginula*, *Botelloides*, *Sassia*, *Columbarium*, *Cyllichnania*, *Odostomia*, *Acteon* and *Spiratella* occur in the Late Eocene fauna of the Otway Basin, none of the Eocene species seem to be closely related

to the Paleocene. *Marshallaria* occurs in the Early Oligocene and *Conominolia*, *Zemacies*, *Tenuiactaeon* and *Raulinia* occur in the Late Oligocene. *Fusinus* (Eocene taxa are very small and probably not related), *Proximitra* and *Gadila* are known from the Miocene.

Pebble Point genera not found above the Paleocene in Australia include *Rinula*, *Puncturella*, *Guildfordia* (*Opella*)?, *Euspira*, *Colposigma*, *Pseudofax* (unless it proves to be a synonym of *Cominella*), *Levifusus*?, *Microfulgur*?, *Pseudoliva* (*Buccinorbis*), *Cosmasyrinx* (*Tholotoma*), *Tornatellaea*, *Gilbertina*, *Priscaphander* and *Tuba*. *Pseudoliva* (*B.*) may be ancestral to the Australian endemic genus *Zemira* (Early Oligocene–Recent).

Genera previously known only from the Australian Recent fauna are *Compressidens* and *Calliotropis*.

LOCALITIES

The details of the localities from which material was collected are as follows. The numbers are from the Museum of Victoria fossil locality register and are used throughout to save repetition. The locality details given in Darragh (1994) contained erroneous grid references for localities PL3003, PL3004, PL3176 and PL3177 which are corrected here.

Pebble Point Formation

PL3001 SE side of Dilwyn Cove, N side of Bell Point, 6 km SE of Princetown, from boulders on beach derived from 0.5 m grey (weathered) sandstone about 15 m above beach, Victoria, Princetown 903100.

PL3002 N side of Dilwyn Cove, S side of Pebble Point, G.S.V. loc. Aw6, 5 km SE of Princetown, Victoria, Princetown 900103.

PL3003 Cove between Buckley Point and Point Pember, 4.5 km SE of Princetown, Victoria, Princetown 896106.

PL3004 Shelly band about 10 m above beach, NW side of Buckley Point, 4 km SE of Princetown, Victoria, Princetown 894110.

PL3005 W end of large slip at Killara Bluff at top section, allot. 4, sect. A, Parish of Killara, Victoria, Dartmoor WD313291.

PL3006 Ironstone about 100 m above river, right bank of Glenelg River on Hazell Bank, Bahgallah, Victoria, Dartmoor WD324296.

PL3176 Cutting on Morgiana Road, about 5 km south of Wannon, left bank Grange Burn, Coleraine WD760267.

PL3177 South flowing gully running into right bank of Grange Burn, about 0.5 km south of Clayton's Road, 3.5 km southeast of Wannon, Coleraine WD729253.

Dilwyn Formation, Rivernook Member

PL3007 Middle of Rivernook Beach, SE side of where track comes down, 0.4 km SW of Rivernook Victoria, Princetown 888119.

Dilwyn Formation, Trochocyathus band

PL3009 G.S.V. loc. Aw7, Rivernook Beach, black silt beneath outcrop of indurated siltstone, 1.5 km SE of Point Ronald, 0.4 km due W of Rivernook, Victoria, Princetown 885123.

Most of the material described here was collected from fallen boulders at PL3001 and PL3003.

SYSTEMATIC DESCRIPTIONS

All specimens are housed in the Invertebrate Palaeontology Collection, Museum of Victoria, register prefix P, except for some specimens housed in the Western Australian Museum, register prefix WAM.

Abbreviations used in citing dimensions are L (length), H (height), HA (height of aperture), W (width).

Class Gastropoda

Family FISSURELLIDAE

Emarginula Lamarck, 1801

Type species. E. conica Lamarck, 1801 (= *fissura* Linnaeus, 1758) Recent, Europe.

Emarginula sp.

Fig. 1N

Description. Shell small for genus (2×1.8 mm), cap shaped, high, narrow, apex above posterior margin. Sculptured with coarse, widely spaced radial ribs, eight on half of shell, and nine strong, well spaced colabral costae, giving shell a coarsely fenestrate appearance. Selenizone bounded on each side by narrow ribs and filled with thin widely spaced septa.

Dimensions

Figured specimen P302610 L 2.0 W 1.8 (est.)

Figured material. Figured specimen P302610, collected T. A. Darragh, 18 January 1996.

Occurrence. PL3003 (1 specimen).

Remarks. The single specimen is a worn fragment, consisting of about half the shell. It is somewhat similar to *Emarginula grata* Makarenko, 1976, Paleocene, Ukraine, in its coarse sculpture, but does not have the quadrate outline of that species and the radial ribs are all of equal strength unlike *E. grata*. It is also similar to *E. beclardi* Cossmann, Paleocene, Belgium but has fewer colabral costae.

Emarginula occurs in the Danian and Paleocene of Europe (Ravn 1939; Glibert 1973; Makarenko 1976), the Paleocene of Pitt Island, New Zealand (Campbell et al. 1993) and has a cosmopolitan distribution from Eocene to Recent. In Australia the genus was previously known from Late Eocene through to Recent. The Eocene species have much finer sculpture than this Paleocene taxon.

Rimula Defrance, 1827

Type species. *Rimula blainvilli* Defrance, 1827, Eocene, France.

Rimula? crepiduloides sp. nov.

Figs 1K, M, 11B–C, E–F

Description. Shell small (1.7×2.6 mm), thin, cap shaped, smooth. Apex close to posterior margin. Slit closed anteriorly and with long hole on anterior $\frac{2}{3}$ of shell. Small septum present. On largest specimen apex coiled round twice with shelf visible inside coiling.

Dimensions

Holotype P302613	H 1.3	L 2.6	W 1.5
Paratype P302612	1.2	2.0	
Paratype P302007	1.8 approx.		1.7 approx.

Type material. Holotype P302613 and Paratype P302612, collected T. A. Darragh, 18 January 1996; Paratype P302007, collected T. A. Darragh, 24 November 1992; Paratype P302008, collected T. A. Darragh, 13 December 1994.

Type locality. PL3003.

Occurrence and material. PL3003 (21 specimens).

Remarks. Of the 21 specimens only five are possibly adult specimens, the others are almost certainly juveniles. A large fragment showing portion of the slit band with hole indicates that most of the reasonably complete specimens are about half the size of the fragment if it were complete.

This species is similar in size and shape to *Rimula praeintorta* Rutot in Cossmann, 1913,

Paleocene of Mons, but *R. praeintorta* has fine spiral lirae covering the whole whorl. *R. crepiduloides* seems to be related to species of *Rimula* from the Eocene of the Paris Basin, but these do not show the shelf on published illustrations, possibly because it is very small and very close to the coiled apex and hence out of sight. *R. crepiduloides* looks similar to *R. nincki* Cossmann, Cuisian, Paris Basin, in shape and lack of sculpture, but the latter is said not to have a shelf. The largest of the Pebble Point specimens has the shelf hidden back in the coiled apex and is only visible because the side of the shell is broken.

Puncturella (Altrix) Palmer, 1942

Type species. *Fissurella altior* Meyer & Aldrich, 1886, Middle Eocene, United States of America.

Puncturella (Altrix) *caminata* sp. nov.

Fig. 1P–Q, Y

Description. Shell small, conical, high, ovate in outline, wider anteriorly. Apical perforation key-hole shaped. Sculptured with strong radiating ribs, slightly narrower than interspaces (28–31); thinner ribs between most primary ribs (17–26). Ribs bearing low tubercles where crossed by strong concentric growth lines. Internal septum present against anterior side of apical perforation.

Dimensions

Holotype P302006	L 1.5	W 1.1	H 0.8
Paratype P302614	1.9	1.3	1.2
Paratype WAM 94.404	1.9	1.3	1.2

Type material. Holotype P302006, collected T. A. Darragh, 13 December 1994. Paratype P302614, collected T. A. Darragh, 18 January 1996. Paratype WAM 94.404, collected G. W. Kendrick, 13 November 1984.

Type locality. PL3003.

Occurrence and material. PL3003 (6 complete specimens and three fragments).

Remarks. This species looks very like *Puncturella* (Altrix) *altior* (Meyer & Aldrich), Middle Eocene, southeastern USA, but is not so heavily sculptured. There does not seem to be any taxa quite like this in the Paleocene of Europe or New Zealand or the Eocene of Antarctica, having such a tall conical shape.

Family COCCULINIDAE

Cocculina Dall, 1882

Type species. *C. rathbuni* Dall, 1882, Recent, north-western Atlantic.

Cocculina? sp.

Fig. 1L, O

Description. Shell of average size for genus (2×1.5), high, cap-like, narrowly elongate-oval, with subparallel sides. Apex of shell situated slightly posterior of mid point. Protoconch broken, trace preserved on posterior.

Dimensions

Figured specimen P302609 H 2.0 W 1.5 L 2 (est.)

Figured material. Figured specimen P302609, collected T. A. Darragh, 18 January 1996.

Occurrence and material. PL3003 (1 specimen).

Remarks. The internal surface of the shell is not visible and preservation of the specimen is not good enough to be absolutely certain of the generic assignment. In addition many of the characters used to distinguish genera in this family are based on anatomical features not available in fossil material. This species bears some resemblance to *Cocculina cervae* Fleming, 1948, Recent, New Zealand and *C. pristina* Marshall, 1985, Miocene, New Zealand (Marshall 1985), but the Pebble Point specimen lacks any trace of radial sculpture. Members of the family have a cosmopolitan distribution, mostly in deep water, but *C. cervae* is found in depths ranging from 18 to 891 m. Living species feed on decayed wood. Fossil species have been recorded from the Miocene of Europe, West Indies and New Zealand. It is possible that some of the cap-shaped species recorded from the Palaeogene of Europe as *Acmaea* may belong in *Cocculina*.

Family TROCHIDAE

Calliotropis Seguenza, 1903

Type species. *Trochus otto* Philippi, 1844, Pleistocene, Italy.

Calliotropis microglyptophorus sp. nov.

Fig. 2C, Q-T

Description. Shell conical, small (9–12 mm), nacreous of five to seven flat whorls with deeply impressed sutures. Protoconch of one whorl, smooth, somewhat globosic, coiled at slight deviation to axis of shell.

First teleoconch whorl convex, bearing widely spaced costae, keel developing on second teleoconch whorl. Spire whorls with three prominent and widely spaced lirae; anterior lira most prominent and forming pronounced keel. Last whorl with three prominent lirae and anterior to keel another five widely spaced strong lirae.

Axial sculpture of regularly and widely spaced costae extending from posterior suture to keel, sharply nodulate where crossed by spiral lirae; costae not present anterior to keel on last whorl, 18–22 on last whorl. Microsculpture of dense, wavy, prosocline lamellae.

Aperture subcircular, internal lip smooth. No umbilicus.

Dimensions

	H 9.5	W 6.2	HA 3.0
Holotype P301884			
Paratype P301885	9.0	6.4	3.0
Paratype P301886	12.0	9.0	—

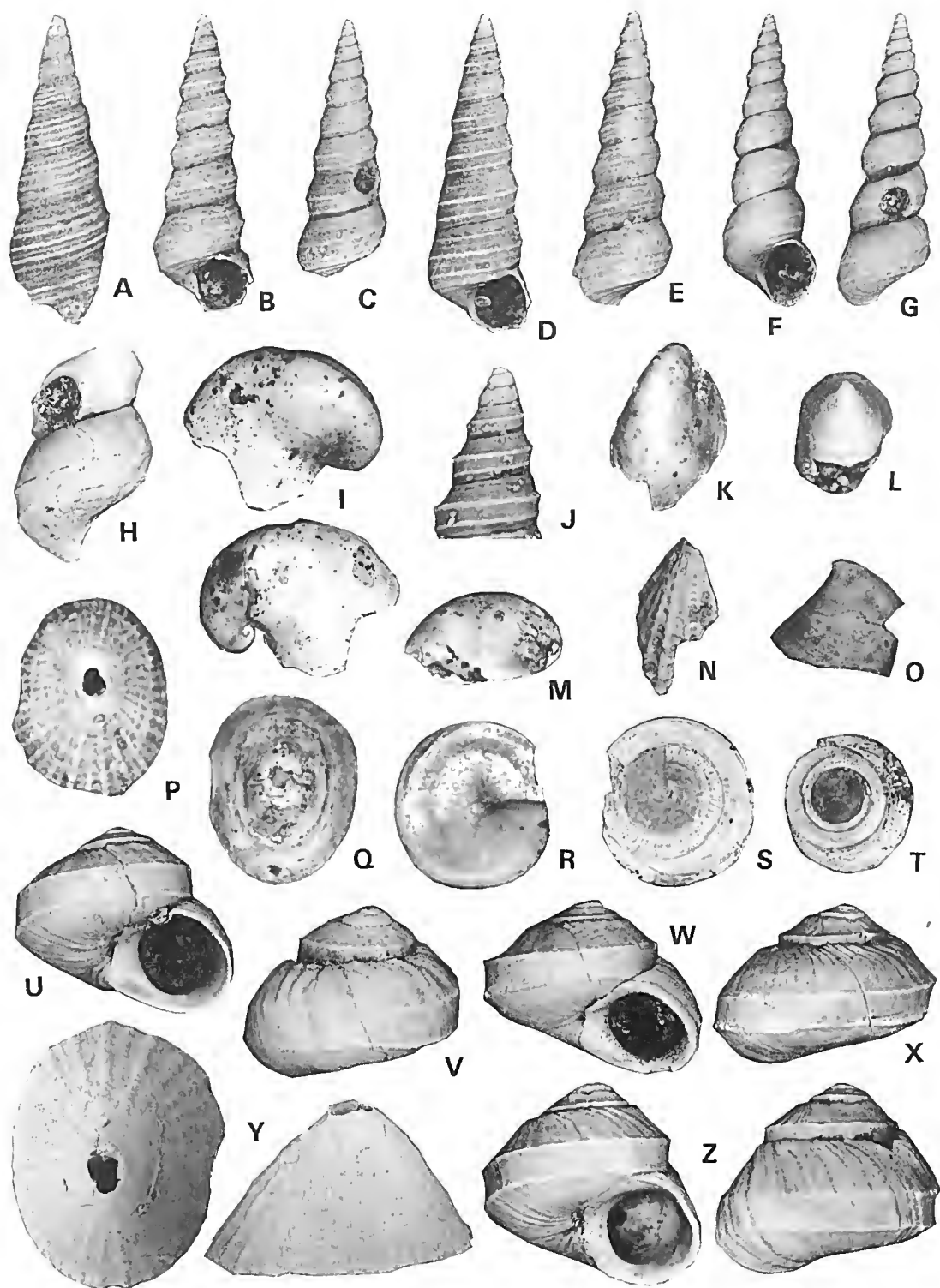
Type material. Holotype P301884, collected T. A. Darragh, 17 February 1981; Paratype P301885, collected T. A. Darragh, 8 May 1979; Paratype P301886, collected T. A. Darragh, 13 November 1984. Paratype WAM 94.409, collected G. W. Kendrick, 13 November 1984.

Type locality. PL3003.

Occurrence and material. PL3001 (7 specimens), PL3003 (14 specimens), PL3004 (1 specimen), Pebble Point area unlocalised (2 specimens).

Remarks. I follow Marshall (1979) in his concept of the genus, which includes species that range from having a wide umbilicus to those with no umbilicus.

Fig. 1. A, Turritellid, NMV P301904, figured specimen, PL3001, ×4.9. B–H, J, *Colposigma uniangulata* sp. nov. B–C, J, NMV P301902, paratype, PL3003, B, ×5.1, C, ×4.0, D, ×12.5. D–E, NMV P301901, holotype, PL3003, ×3.9. F–H, P301903, paratype, PL3003, F–G, ×4.1, H, ×6.8. I, K, M, *Rimula crepiduloides* sp. nov. I, NMV P302007, paratype, PL3003, ×15.0. K, M, NMV P302008, paratype, PL3003, ×20. L, O, *Cocculina?* sp., NMV P302609, figured specimen, PL3003, ×7.1. N, *Emarginula* sp., NMV P302610, figured specimen, PL3003, ×11.8. P–Q, Y, *Puncturella (Altrix) caminata* sp. nov., NMV P302006, holotype, PL3003, P–Q, ×20. Y, ×27. R–X, Z, *Cirsochilus pilulatus* sp. nov. R–S, possible operculum, NMV P301899, figured specimen, PL3003, ×13.2. T, possible operculum, NMV P301899, figured specimen, PL3003, ×14. U–V, NMV P301896, holotype, PL3003, ×6.6. W–X, NMV P301897, paratype, PL3003, ×6.6. Z, NMV P301898, paratype, PL3003, ×6.2.



The recent species of the genus have a cosmopolitan distribution in deep water, but the fossil record is very fragmentary. Species occur in the Paleocene of Denmark (*Calliotropis oedumi* (Ravn)), Early Oligocene of Germany, (*C. bundensis* (v Koenen)) and Pleistocene of Italy, (*C. otto* (Philippi)). In New Zealand, species have been found ranging in age from Late Eocene to Recent. *Calliotropis microglyptophorus* is somewhat similar *C. bundensis* (von Koenen), but that species has weak axial ribbing on the base and is much smaller. It also bears some resemblance to *C. acherontis* Marshall, Recent, Kermadec Islands and east coast of New South Wales and Queensland, but is much larger, not so narrow and has a more prominent midwhorl keel.

In Australia the genus is not known from younger Tertiary rocks, but several species have been recorded from deep water off the east coast of Australia by Jansen (1994).

Bathymophila Dall, 1881

Type species. Margarita euspira Dall, 1881, Recent, Caribbean.

***Bathymophila? bystromphalata* sp. nov.**

Fig. 2A–B, F–H

Description. Shell small to medium size (7×7–1×1 mm), nacreous, conical, spire subgradate with very narrow horizontal ramp against posterior suture. Protoconch planorboid of two smooth whorls coiled with axis of shell. Whorl shoulder bearing closely spaced nodules.

Spiral sculpture of few thick lirae; two or three on spire whorls against anterior suture, on some specimens two weaker lirae between these and shoulder. Lirae on some specimens beaded. On some specimens weak lirae on ramp. Last whorl with up to five lirae clustered at whorl periphery. Base smooth. Umbilicus encircled by two lirae bearing close set nodules. No axial sculpture.

Aperture subcircular, outer lip prosocline. Inner lip with thin callus extending over and plugging umbilicus. Umbilical plug on many specimens damaged or missing.

Dimensions

Holotype P301887	H 8.8	W 9.8	HA 4.2
Paratype P301888	6.9	7.7	4.1
Paratype P301889	9.5	8.8	4.2

Type material. Holotype P301887, collected T. A. Darragh, 24 November 1992; Paratype P301888, collected T. A. Darragh, 28 February 1970; Paratype P301889, collected T. A. Darragh, 17 February 1981.

Type locality. PL3003.

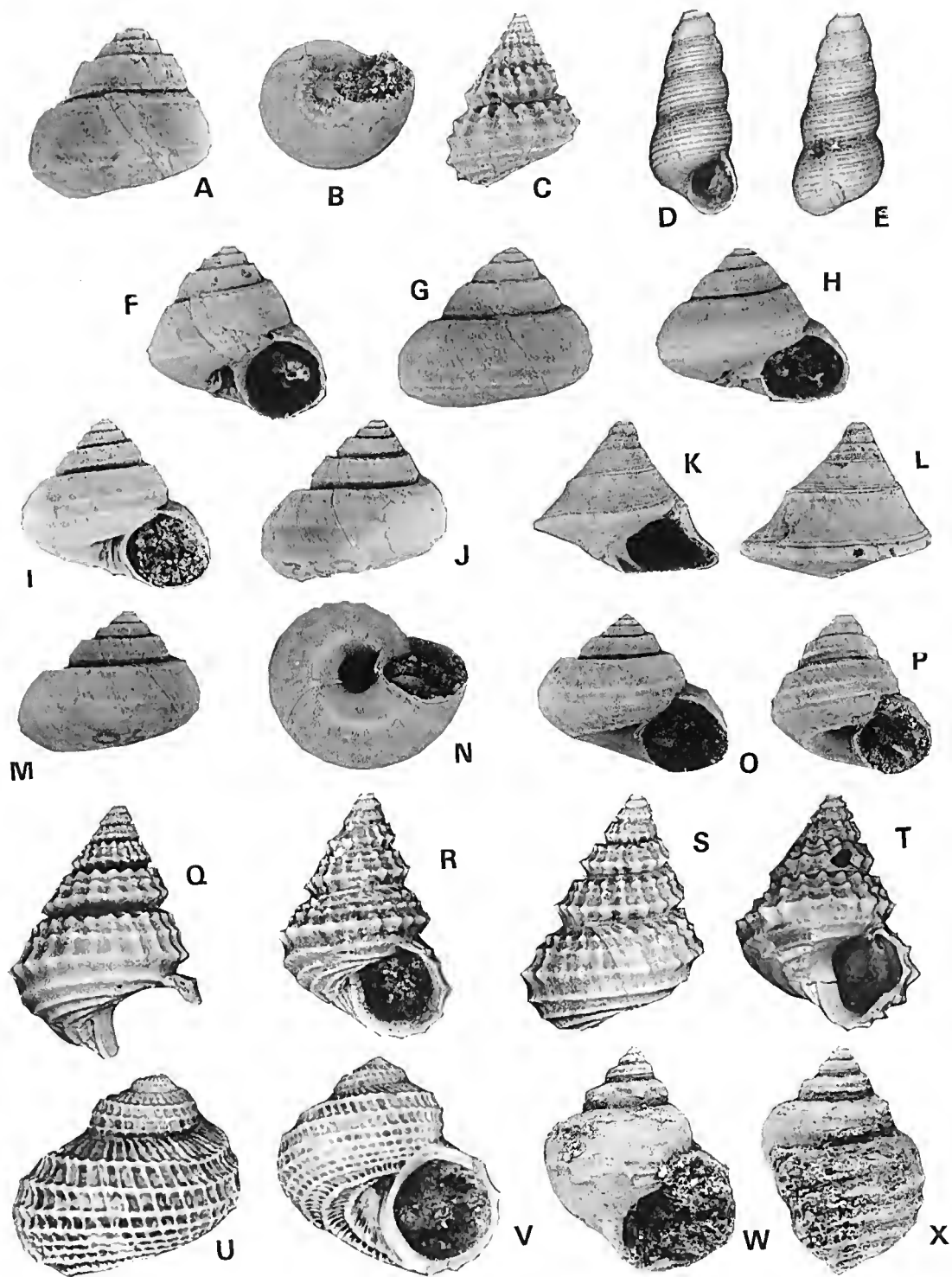
Occurrence and material. PL3001 (5 specimens), PL3003 (17 specimens), PL3001 (1 specimen).

Remarks. Most specimens are decorticated to some extent and have the umbilical plug missing. There is nothing like this taxon in the New Zealand Paleocene or Antarctic Eocene. I have placed this species provisionally in *Bathymophila* because it has considerable resemblance to *Bathymophila bairdi* (Dall, 1889), Recent, Florida.

Bathymophila? bystromphalata sp. nov. can be confused with *Conominolia parvistrigulata* sp. nov. because it has a somewhat similar shape, but the whorl shoulder of *B. bystromphalata* is strongly beaded up to the aperture, the umbilicus is plugged, and there are no numerous fine spirals, only three or four fine cords at the maximum convexity on the last whorl, the strongest of which is on the spire whorls close to the anterior suture. *Conominolia parvistrigulata* has a more gradate spire.

Bruce Marshall (in litt.) draw my attention to this species' similarity to species of *Lamellitrochus* Quinn, 1991. The shape is somewhat similar, but species of *Lamellitrochus* do not seem to have a plugged umbilicus and all species have lamellate axial riblets on the early teleoconch whorls which are lacking in *B. bystromphalata*. He also pointed out that *Trochus marginulatus* Philippi, 1844, Pleistocene, Sicily, is very similar in shape and sculpture. This latter species has an umbilicus

Fig. 2. A–B, F–H, *Bathymophila? bystromphalata* sp. nov. A, F, NMV P301889, paratype, PL3003, ×2.7. B, NMV P301888, paratype, PL3001, ×3.1. G–H, NMV P301887, holotype, PL3003, ×2.8. C, Q–T, *Calliotropis microglyptophorus* sp. nov. C, T, NMV P301885, paratype, PL3003, C, ×2.8, T, ×3.9. Q, NMV P301886, paratype, PL3003, ×3.3. R–S, NMV P301884, holotype, PL3003, R, ×3.9, S, ×3.8. D–E, *Botelloides* sp. NMV P301893, figured specimen, PL3003, ×6.6. I–J, M–P, *Conominolia parvistrigulata* sp. nov. I–J, NMV P301892, paratype, PL3003, ×2.2. M–O, NMV P301890, holotype, PL3003, M, ×2.2, N, ×2.4, O, ×2.3. P, NMV P301891, paratype, PL3001, ×2.4. K–L, *Guildfordia (Opella)?* sp., NMV P301894, figured specimen, PL3003, ×2.1. U–V, *Paraeuchelus?* sp., NMV P301900, figured specimen, PL3003, ×10.3. W–X, Turbinid indet., NMV P301895, figured specimen, PL3003, ×2.2.



which is almost but not completely filled with callus.

B. bystromphalata bears some resemblance to *Calliomphalus firketi* (Briart & Cornet), Paleocene, Mons but that species has more numerous lirae and the umbilicus is not plugged.

Conominolia Finlay, 1926

Aura Stewart, 1927: 315.

Garramites Stephenson, 1941: 262.

Type species. *Heliacis conica* Marshall, 1917, Paleocene, New Zealand.

Conominolia parvistrigulata sp. nov.

Fig. 21-J, M-P

Description. Shell of average size for genus (7×7.5–13×11 mm), subconical, nacreous. Protoconch planorbid, smooth, coiled with axis of shell, about 1½ whorls. Teleoconch of five to six whorls. Spire whorls biangulate, flat between angulations, with prominent narrow flat horizontal sutural ramp. Edge of ramp beaded, whorl sloping steeply to second angulation slightly anterior of mid whorl. Whorl slope flat, sutures impressed, third angulation barely visible above anterior suture on some specimens. Last whorl with third angulation at anterior 2/3; whorl rounded and abruptly contracting to base.

Sculpture of fine spiral threads present over whole of spire whorls and last whorl including umbilicus; umbilicus smooth on some specimens. Beading on shoulder becoming weaker anteriorly. No axial sculpture.

Umbilicus wide, conical, bounded by prominent cord bearing coarse beading. Aperture broadly sub-lenticular, angulate on outer lip side, columella subcircular. Outer lip prosocline.

Dimensions

Holotype P301890	H 10.5	W 12.5	HA 5.5
Paratype P301891	11.4	10.1	5.8
Paratype P301892	12.0	13.0	6.5

Type locality. PL3003.

Type material. Holotype P301890, collected T. A. Darragh, 13 December 1994; Paratype P301891, collected T. A. Darragh, 16 February 1981; Paratype P301892, collected T. A. Darragh, 27 November 1972. Paratype WAM 94.405a, collected G. W. Kendrick, 13 November 1984.

Occurrence and material. PL3001 (33 specimens), PL3003 (69 specimens), PL3004 (7 specimens), Pebble Point area unlocalised (13 specimens).

Remarks. Shells of this species are easily decorticated and lose the thin outer shell surface which bears fine spiral threads, thus exposing the nacreous layer and so appearing smooth-surfaced. *Conominolia parvistrigulata* sp. nov. is very similar to the type species of the genus, *C. conica* (Marshall), but differs in having less rounded, flatter and more angular whorls, less developed spiral lirae (finer and more numerous), and beading only on the edge of the ramp. In shape *C. parvistrigulata* is more conical rather than turbiniform as in *C. conica*. *C. sulcatina* (Suter, 1917), late Oligocene, New Zealand, has fewer and much coarser spirals.

Conominolia parvistrigulata is very similar to *C. strigata* (Tenison Woods, 1879), late Oligocene–Middle Miocene, Victoria, but that species is about 2/3 the size of *C. parvistrigulata* for the same number of whorls. *C. parvistrigulata* has coarser beading on the whorl shoulder, and more spiral lirae which are well developed over the whole whorl, whereas on *C. strigata* the lirae are weaker on the base and may be obsolete. *C. strigata* also has much more rounded whorls than *C. parvistrigulata*, that is the angulations are not so well developed, and the aperture is D shaped rather than sublenticular as in *C. parvistrigulata*.

Conominolia ranges in age from Paleocene to Pliocene in New Zealand and in Australia it occurs in the Paleocene and at least from Late Oligocene to Middle Miocene. Species that seem to belong in *Conominolia* occur in the Paleocene (*Delphinula multilineata* Briart & Cornet, 1887) (Glibert 1973) and Eocene (*Turbo odontotus* Bayan, 1873) of Europe and the Late Cretaceous of the United States of America. Finlay & Marwick (1937) suggested that *Atira* Stewart, 1927, type species *Angaria ornatissima* Gabb, late Cretaceous, California, was a synonym of *Conominolia*. I agree with this suggestion. Sohl (1960a) placed several species from the late Cretaceous of the south-eastern United States in the genus *Calliomphalus* Cossmann, 1888 and synonymised *Garramites* Stephenson, 1941 with this genus. The type species, *Garramites nitidus* Stephenson (Stephenson 1941), is very similar to species of *Conominolia*, as are some of the species placed by Sohl in *Calliomphalus*. *Conominolia* is very similar to *Calliomphalus* but I retain the former as there are some differences. Compared with *Calliomphalus squamulosus* (Lamarck), type species of the genus, species of *Conominolia* are more angular in outline, have a gradate spire and the umbilicus is angular and bounded by a beaded cord. *Calliomphalus (Planolateralus)* Sohl, 1960 is somewhat intermediate between *Conominolia* and

Calliomphalus s.s., having a cone shaped spire and prominent axial sculpture like species of *Calliomphalus*. It is similar to *Conominolia* in having an angulate umbilicus bounded by a beaded cord. The two species placed by Sohl in *Calliomphalus* s.s. (*americanus* Wade and *nudus* Sohl) would be better placed in *Conominolia*.

Botelloides Strand, 1928

Type species. *Onoba bassiana* Hedley, 1911, Recent, southern Australia.

Botelloides sp.

Fig. 2D-E

Description. Shell of large size for genus (4.7 mm), elongate, pupiform, solid. Protoconch of about $1\frac{1}{2}$ smooth planorbid whorls, coiled with axis of shell and merging imperceptibly with spire whorls. Teleoconch of $4\frac{1}{2}$ regularly convex whorls. Spiral sculpture of eight coarse, close-set lirae, about 18 on last whorl. Axial sculpture of growth lines only.

Aperture subcircular, outer lip thin, thickened within. Columella covered with thick glaze.

Dimensions

Figured specimen P301893 H 4.7 W 2.0

Figured material. P301893, collected T. A. Darragh, 24 November 1992.

Occurrence and material. PL3003 (1 specimen and 4 fragments).

Remarks. Ponder (1985) has recorded the genus from late Eocene to Recent in Australia and this record extends the range to the Paleocene. Species are found living around the entire coast line of Australia in coarse substrates on the continental shelf or subtidally (Ponder 1985). The Pebble Point species has much more convex whorls than the younger species. Of the Australian species it is most similar to the late Eocene *Botelloides darraghi* Ponder, but it has much more convex whorls and stronger lirae. It has some resemblance to *Halistylus pupoideus* (Carpenter), Recent, California, a species of a related genus known from Pliocene to Recent (Hickman & McLean 1990).

Family TURBINIDAE

Guildfordia (Opella) Finlay, 1926

Type species. *Astraea* (*Uvanilla*) *subfimbriata* Suter, 1917, Early Miocene, New Zealand.

Guildfordia (Opella) ? sp.

Fig. 2K-L

Description. Shell small (11 mm), coeloconoid, nacreous, wider than high. Protoconch of one smooth depressed whorl. Teleoconch of $5\frac{1}{2}$ whorls, first $1\frac{1}{2}$ whorls convex, next $\frac{1}{2}$ whorl flatter, remainder of whorls concave.

Spiral sculpture of low broad lirae, somewhat irregularly distributed across whorl face and better developed closer to anterior suture. One strong thin lira beginning on second teleoconch whorl and extending for $2\frac{1}{2}$ whorls, then fading on fifth whorl. Last whorl with prominent keel at edge of base bearing widely spaced low tubercles. Base with close-set low lirae extending from keel to centre of base.

Aperture trapezoidal, inner lip covered with thin glaze. Outer lip extended behind and in front of columella forming depression between it and columella.

Dimensions

Figured specimen P301894 H 11 W 3.4 HA 4

Figured material. Figured specimen P301894, collected T. A. Darragh, 24 November 1992.

Occurrence and material. PL3003 (1 specimen).

Remarks. This specimen is unlike any other known in Paleocene or Eocene strata. It has some resemblance to species placed in *Astrarium*, *Pomaulax*, *Bellastrea* and *Uvanilla*, but lacks the granular ribs characteristic of most of these. The spire is also uniformly concave unlike many of those species in which each whorl is concave and the suture projects. It comes closest to *Guildfordia* (*Opella*) *subfimbriata* (Suter), type species of the genus, and *Guildfordia* (*Opella*) sp. (Beu & Maxwell, 1990) and so I have placed it provisionally here. It may possibly be ancestral to this taxon. There is nothing like it known from the later Tertiary of Australia.

Turbinidac, gen. et spec. indet.

Fig. 2W-X

Description. Shell small for the genus (14×16 mm), turbiniform with gradate spire. Protoconch of $2\frac{1}{2}$ smooth whorls, first whorl depressed, other whorls convex. Teleoconch of four whorls with prominent shoulder, ramp flat to gently concave.

Spiral sculpture of six to seven weak lirae on ramp, one thick lira on shoulder and two prominent lirae anterior to it on spire whorls. Last whorl with

about 6 prominent lirae anterior to shoulder cord and two fine threads between each pair of cords.
Aperture not preserved. No umbilicus.

Dimensions

Figured specimen P301895 H 16 W 14

Figured material. Figured specimen P301895, collected T. A. Darragh, 17 February 1981.

Occurrence and material. PL3003 (1 specimen).

Remarks. The single specimen is badly decorated on the anterior whorls and the aperture is broken away, so that generic assignment is not possible. In shape and sculpture it looks very like *Turbo radiosus* Lamarck, Eocene, Paris Basin. There is nothing like it recorded from the Paleocene of Europe or New Zealand.

Species of *Turbo* sensu lato are known from the Early Miocene and later in southeastern Australia, but all have less gradate spires, more rounded whorls and prominent beading on the spiral sculpture.

***Cirsochilus* Cossmann, 1888**

Type species. *Delphinula striata* Lamarck, 1804, Eocene, Europe.

***Cirsochilus pilulatus* sp. nov.**

Fig. 1R–X, Z

Description. Shell small, of average size for genus (5.5×4.9–6.2×4.5 mm), solid, turbinate, depressed, nacreous within. Protoconch of about one smooth whorl, not differentiated from teleoconch whorls. Whorls three to four, angulate; each teleoconch whorl almost enveloped by succeeding whorl. Spire whorls with prominent shoulder developed into keel. Last whorl with second anterior keel.

Base of shell on some specimens with three or four widely spaced spiral grooves. Axial sculpture merely of growth lines, somewhat irregularly developed; on some specimens growth lines form ridges against posterior suture.

Aperture circular. Outer lip oblique; inner lip with callus spreading over small umbonal chink.

Possible operculum, calcareous, subcircular, paucispiral, calcified pad smooth, centre of operculum missing (possibly corneous, multispiral).

Dimensions

Holotype P301896	H 4.2	W 5.0	HA 2.2
Paratype P301897	3.9	5.0	2.0
Paratype P301898	5.5	5.5	2.2

Type material. Holotype P301896, Paratype P301897, Paratype P301898, Figured opercula P301899, all collected T. A. Darragh, 13 December 1994. Paratype WAM 94.406, collected G. W. Kendrick, 13 November 1994.

Type locality. PL3003.

Occurrence and material. PL3001 (29 specimens), PL3003 (214 specimens), PL3004 (18 specimens), Pebble Point area unlocalised (5 specimens).

Remarks. *Cirsochilus pilulatus* sp. nov. is very similar to the type species, *Cirsochilus striatus*, but that species has numerous spiral lirae in addition to the keels, as well as a wider umbilicus. *C. pilulatus* has only an umbilical chink which is covered in most specimens. *Tipua* Marwick, type species *Submargarita tricineta* Marshall, Eocene, New Zealand, scarcely differs from *Cirsochilus* and the cited differences, lack of a border to the outer lip, a smaller umbilicus, and the spreading parietal callus, seem minor. *C. pilulatus* is similar in morphology to *Tipua tricineta* but lacks the spiral threads between the keels of that species.

The genus is widespread in the Eocene and Oligocene of Europe and the Eocene of the United States of America, but has not been recorded from the Eocene of Antarctica, nor from the Paleocene of New Zealand, northern Europe or the United States of America. It occurs in the Eocene (assuming *Tipua* is a synonym) and Miocene of New Zealand. It has *C. pilulatus* is very similar to *Solariella parva* Makarenko, Paleocene, Ukraine, but that species has a wider umbilicus.

***Pareuchelus* Boettger, 1907**

Type species. *Euchelus* (*Pareuchelus*) *excellens* Boettger, 1907, Miocene, Hungary.

***Pareuchelus* ? sp.**

Fig. 2U–V

Description. Shell small (3.4×3.3 mm), turbinate-form. Protoconch damaged, of one or two whorls, coiled in axis of shell. Teleoconch whorls three with narrow sutural ramp bounded by sharp shoulder.

Spiral sculpture of prominent sharp well spaced lirae, one at shoulder, one at anterior suture and one midway between these two. Nine lirae on last whorl, two closest to umbilicus stronger than others. Axial sculpture of narrow sharp costae, slightly narrower than lirae, extending from suture

to suture on spire and on last whorl from suture into umbilicus; slightly nodulate on crossing lirae.

Aperture subcircular, broken. Umbilicus prominent, deep.

Dimensions

Figured specimen P301900 H 3.3 W 3.4

Figured material. Figured specimen P301900, collected T. A. Darragh, 2 December 1985.

Occurrence and material. PL3003 (1 specimen).

Remarks. This species resembles *Pareuchelus lefevrei* Rutot in Cossmann, 1915, Paleocene, Mons, but it is squatter and the axial costae are not so strong. It is also very similar to *P. cancellatocostatus* (Sandberger), Rupelian, Germany, but it has a small umbilicus rather than the mere umbilical chink present in that species. The genus occurs in central Europe from Paleocene to Middle Miocene. It is not known from northern Europe.

Family TURRITELLIDAE

Colposigma Finlay & Marwick, 1937

Type species. *Colposigma mesalia* Finlay & Marwick, 1937, Pliocene, New Zealand.

The terminology used in the description of the following species is that of Marwick (1957).

Colposigma unianguata sp. nov.

Fig. 1B–H, J

Description. Shell of average size for genus (3.7×11.8–3.9×13.5 mm) with narrow prominently keeled spire whorls. Protoconch polygyrate of 3½ smooth, swollen, very convex whorls coiled with axis of shell. Teleoconch of nine to ten whorls. First teleoconch whorl with two spirals (B and C), B central and C anterior develop together, B stronger and develops rapidly into prominent keel. Second whorl with spiral A appearing against posterior suture and spiral D against anterior suture. Third whorl on some specimens with very weak lirae developing between A and B. Fourth whorl with fine spiral appearing between C and D. Base with three to four fine lirae anterior to D. Last whorl on most specimens regularly rounded and not keeled.

Apertural sinus deep, apex between posterior suture and mid whorl.

Dimensions

Holotype P301901	H 11.5	W 3.8
Paratype P301902	9.5	3.0
Paratype P301903	11.0	3.6

Type material. Holotype P301901, Paratype P301902, both collected T. A. Darragh, 24 November 1992; Paratype P301903, collected T. A. Darragh, 8 March 1977.

Type locality. PL3003.

Occurrence and material. PL3001 (42 specimens), PL3003 (91 specimens), PL3004 (8 specimens).

Remarks. Specimens are very common in the formation but it is difficult to collect unbroken specimens. Most specimens show signs of abrasion.

The genus was first described from New Zealand and ranges there from Paleocene to Eocene. It is not known from the Eocene in Australia. Marwick (1957) recognised that *Colposigma* occurred in Australia, based on material from the Pebble Point Formation. Compared with *Colposigma mesalia* Finlay & Marwick, *C. unianguata* sp. nov. has more angulate whorls, because the central spiral (B) is more prominently developed giving the shell an angular appearance. *C. unianguata* has five or more spirals not four as in *C. mesalia*. Neither *C. plebeia* Marwick, 1960 nor *C. imparicincta* Finlay & Marwick, 1937 are keeled and *C. unicingulata* bears no resemblance to them.

Turritellid gen. & spec. indet.

Fig. 1A

Description. Shell turriculate with incised sutures. Protoconch missing. Teleoconch whorls convex. Spiral sculpture of five lirae. Aperture broken, growth lines not visible.

Dimensions

Figured specimen P301904 H 9.5 W 3.5

Figured material. Figured specimen P301904, collected T. A. Darragh, 21 November 1970.

Occurrence. PL3001 (1 specimen).

Remarks. The single specimen is broken and worn, so it is not possible to trace the development of the spirals. Superficially the specimen has some resemblance to specimens of *Colposigma mesalia* and also to species of *Spirocolpus*, but the preservation is so poor that detailed comparison is not possible.

Naticidae

Euspira Agassiz, 1837

Type species. *Natica glaucinoides* Eocene, Europe.

Euspira saxosulensis sp. nov.

Fig. 3O–R, V

Description. Shell small, of average size for genus (11×11.2–17×17.5 mm) solid, smooth, globose. Spire somewhat squat and subgradate. Protoconch of one whorl, depressed, not separated from spire whorls. Teleoconch of four whorls, regularly convex. Last whorl very large.

Aperture ovate, outer lip rounded, moderately prosocline, inner lip with very little callus. Umbilicus open, no funicle or callus.

Dimensions

Holotype P301906	H 12.0	W 10.5	HA 9.5
Paratype P301907	12.1	11.5	7.5
Paratype P301908	17.0	16.0	14.0

Type material. Holotype P301906, collected T. A. Darragh, 2 December 1985; Paratype P301907, F. A. Cudmore Collection 1941–46; Paratype P301908, collected T. A. Darragh, 21 November 1970.

Type locality. PL3003.

Occurrence and material. PL3001 (10 specimens), PL3003 (15 specimens), PL3004 (6 specimens), Pebble Point area unlocalised (1 specimen).

Remarks. This and the next two species are probably responsible for the bore holes present in the bivalves from this formation (Darragh 1994). Specimens are reasonably common but in most cases very poorly preserved, owing to decortication of the shell.

This species is very similar to *Euspira fyfei* (Marwick, 1924), Paleocene, New Zealand, but *E. saxosulensis* is much smaller, does not have a sutural channel and the whorls are not quite so regularly convex and swollen. Somewhat similar species occur in the Paleocene of Copenhagen, Mons and United States of America. *E. saxosulensis* is similar in shape to *E. cantiana* Wrigley, 1949, Paleocene, England, but has less callus on the columella.

Naticid sp. a

Description. Shell of average size (13×15–

20×22 mm), spire somewhat conical. Whorls slightly depressed at posterior suture. Aperture D shaped, internal lip of aperture straight, callus well developed. Umbilicus open, covered a little by callus. No funicle.

Occurrence. PL3001 (21 specimens), PL3004 (1 specimen).

Remarks. The available material is poorly preserved and consists mostly of small juvenile specimens. It is not possible to determine if more than one taxon is present. The specimens are readily separated from those of *Euspira saxosulensis* sp. nov. by the conical spire and presence of considerably more callus on the columella.

Naticid sp. b

Description. Shell small (11.7×9.0 mm), solid, smooth, somewhat auriform. Spire scarcely projecting. Teleoconch of about 4 whorls. Aperture D shaped. Parietal callus confined to posterior portion of inner lip. Umbilicus wide, no funicle.

Dimensions

P301909	H 9	W 11.7
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Occurrence and material. PL3004 (1 specimen).

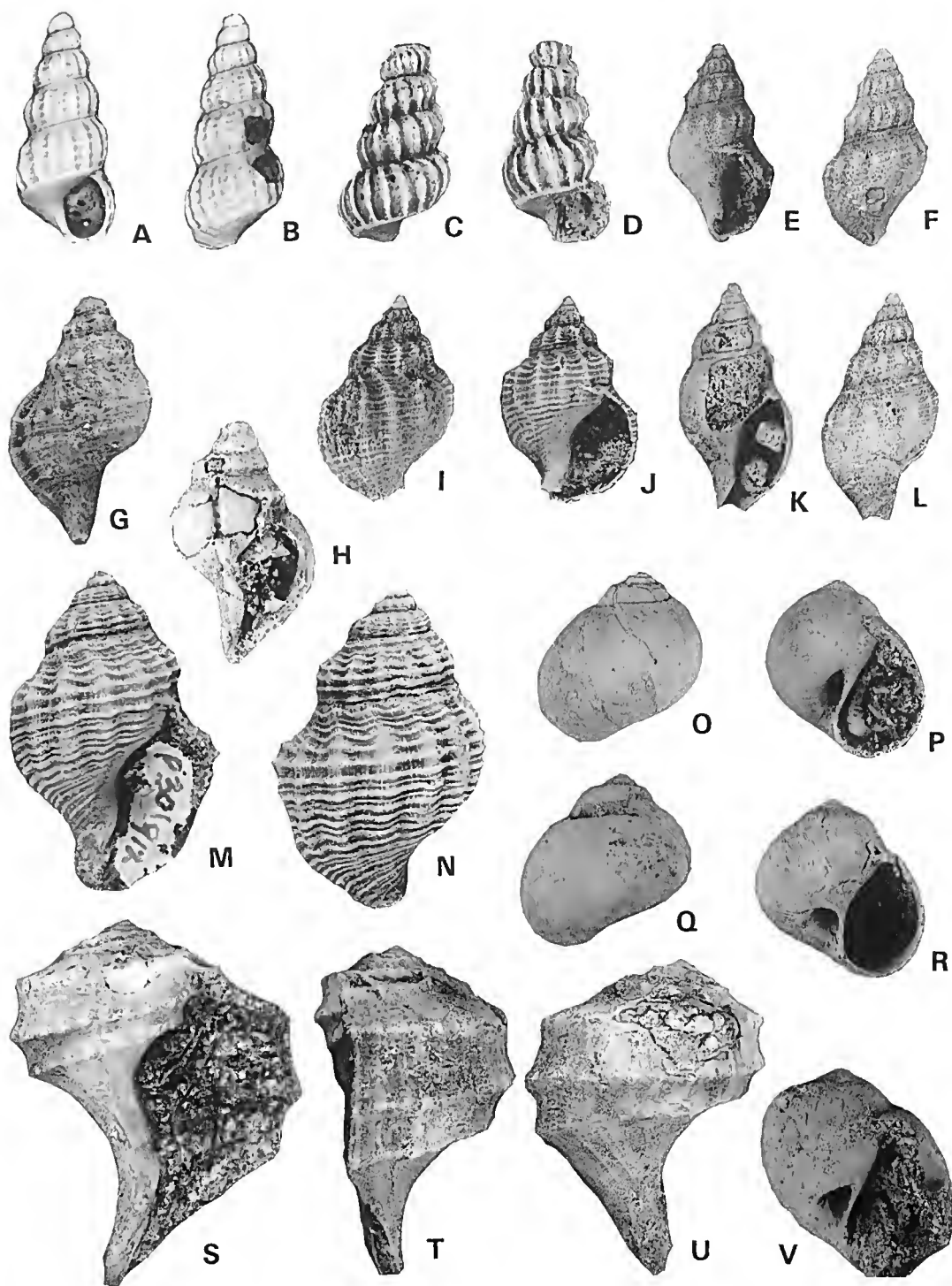
Remarks. The specimen is not well preserved, being slightly decorticated as are many specimens from this locality. It has a large naticid borehole on the ventral side of the last whorl. In shape this taxon resembles species of *Eunaticina* but species of that genus possess spiral sculpture which may not be preserved on this specimen.

Family RANELLIDAE

Sassia Bellardi, 1872

Type, species. *Triton apenninica* Sassi, 1872, Miocene–Pliocene, Italy.

Fig. 3. A–B, Epitoniid, NMV P301911, figured specimen, PL3003, ×10.8. C–D, *Opalia (Pliciscala)?* sp., NMV P301910, figured specimen, PL3004, ×3. E–F, K–L, *Pseudofax* cf. *ordinarius* (Marshall). E–F, NMV P98418, figured specimen, ×2.3. K–L, NMV P301914, figured specimen, PL3001, ×2.3. G–H, *Sassia* sp., NMV P301905, figured specimen, PL3001, ×1. I–J, M–N, *Austrofusus? crassiaulatus* sp. nov. I–J, NMV P301913, paratype, PL3001, ×2.4. M–N, NMV P301912, holotype, PL3001, ×2.2. O–R, V, *Euspira saxosulensis* sp. nov. O–P, NMV P301906, holotype, PL3003, ×2.2. Q–R, NMV P301907, paratype, Pebble Point, ×2.1. V, NMV P301908, paratype, PL3001, ×1.8. S–U, *Levifusus quadrifunifer* sp. nov., NMV P301915, PL3001, S, ×0.64, T–U, ×0.55.



Sassia sp.

Fig. 3G-H

Description. Shell of average size for genus (20×37 mm), fusiform with carinate whorls. Protoconch not preserved. Teleoconch whorls with prominent shoulder with edge situated close to anterior suture. Last whorl with second weaker angulation slightly anterior to shoulder, contracted abruptly anteriorly and produced into short twisted canal. Varices long, narrow, at each $\frac{2}{3}$ of whorl, only two visible, one at aperture and second near beginning of last whorl.

Spiral sculpture of narrow widely spaced fine lirae over whole whorl and two thicker cords, one on shoulder edge and second anterior to it forming a slight keel on last whorl. Axial sculpture of low costae, virtually obsolete on shoulder ramp, but developed into prominent tubercles where they cross spiral cords, not present on last whorl anterior to shoulder.

Aperture oval, outer lip thickened into varix, produced anteriorly into short, left deflected siphonal canal. Inner lip with callus and numerous ridges on columella.

Dimensions

Figured specimen P301905 W 20 H 37 est.

Figured material. Figured specimen P301905, collected T. A. Darragh, 28 November 1972.

Occurrence and material. PL3001 (1 incomplete specimen).

Remarks. *Sassia* has a cosmopolitan distribution. In Europe it is known from Paleocene to Pliocene. In New Zealand it is known from Eocene to Recent. European species of *Sassia* have rounded whorls, whereas the Pebble Point species has angular whorls. In this respect it resembles *Monocirsus carinulatus* Cossmann, Lutetian, Paris Basin, but that species has only one varix and the Pebble Point species has a second anterior keel on the last whorl lacking on *M. carinulatus*. Species of *Sassia* are common in southeastern Australia ranging from Eocene to Recent. In size and shape *Sassia* sp. resembles *Sassia* (*Austrotriton*) *annectens* (Tate) from the Middle Miocene of Victoria. It may be ancestral to *Sassia oligostira* (Tate) from the Late Eocene of Victoria and South Australia. It differs from this species by being larger and having a well developed keel on the shoulder and the cord anterior to the shoulder is much stronger than the equivalent lira on *S. oligostira*.

Sassia sp. has been recorded from the Late Paleocene of Pitt Island, New Zealand (Beu &

Maxwell 1990), but that species does not have the prominent shoulder of the Pebble Point taxon and has relatively well developed axial sculpture.

Family EPITONIIDAE

Opalia (*Pliciscala*) Boury, 1887

Type species. *Scalaria gouldi* Deshayes, 1861, Eocene, Paris Basin.

Opalia (*Pliciscala*) ? sp.

Fig. 3C-D

Description. Shell of moderate size for genus (5×10+ mm), elongate. Protoconch and early spire whorls missing. Whorls strongly convex, sutures impressed. Basal disc well developed on last whorl.

Axial sculpture of prominent narrow, well raised, slightly sinuous costae, extending from suture to suture on spire whorls and on last whorl terminating at prominent spiral cord bounding basal disc; 17 costae on last whorl. Spiral sculpture of very weak threads.

Aperture circular; outer lip continuous truncated at base, produced anteriorly against columella.

Dimensions

Figured specimen P301910 H 10+ (broken) W 5

Figured material. Figured specimen P301910, collected T. A. Darragh, 20 October 1971.

Occurrence and material. PL3003 (1 whorl fragment), PL3004 (1 specimen).

Remarks. There is nothing like this taxon in the New Zealand Paleocene or Late Eocene of Antarctica. Somewhat similar species have been recorded from the Paleocene of Belgium and Ukraine (*Acrilla tournoueri* (Briart & Cornet) and *Opalia wateleti* (Briart & Cornet)) (Makarenko 1976); from the Paleocene of Greenland (*Opalia* sp.) (Kollmann & Peel 1983); and from the Early to Late Oligocene of Germany *Opalia* (*Pliciscala*) *exigua* (von Koenen) and *O. (P.) pusilla* (Philippi) (von Koenen 1891; Janssen 1978).

Opalia (*Pliciscala*)? sp. is somewhat similar to *Opalia* (*O.?*) *fistulosa* Sohl (1964), Late Cretaceous, southeastern United States of America, but the Pebble Point species has much more rounded whorls and impressed sutures. It is similar to *Opalia australis*, type species of the genus, but the whorls are more convex, hence the sutures are more impressed and there are more axial costae.

Epitoniidae, gen. et spec. indet.

Fig. 3A-B

Description. Shell small (1.5×4.5 mm), narrowly conical. Protoconch of 1½ smooth, swollen whorls. Teleoconch of four to five convex whorls, slightly concave at posterior suture. Sutures slightly impressed.

Spiral sculpture of four to five lirae, narrower than interspaces, not present on posterior depressed area. Axial sculpture of strong costae, weakly developed on posterior depressed area, 17 to 20 on last whorl.

Basal disc bounded by sharp lira, visible on spire whorls against anterior suture. Basal disc bearing three or four very weak lirae. Aperture subcircular, peristome discontinuous.

Dimensions

Figured specimen P30191	H 3.2	W 1.3
Measured specimen P302640	4.5	1.5

Figured material. Figured specimen P301911, collected T. A. Darragh, 24 November 1992.

Occurrence and material. PL3003 (2 specimens).

Remarks. These two specimens may possibly be juveniles of *Opalia (Pliciscala)?* sp., however, the most complete specimen of the latter lacks the juvenile whorls making comparison difficult. The posterior part of this specimen of *Opalia (Pliciscala)?* sp. does not closely resemble the largest of these two small specimens, having fewer and more prominent sharp costae which extend from suture to suture, unlike these specimens which have a relatively smooth concave area against the posterior suture.

There is nothing like this recorded from the Paleocene of New Zealand or the late Eocene of Antarctica.

Family BUCCINIDAE

Austrofusus Kobelt, 1879

Type species. *Drupa glans* Roeding, 1798, Recent, New Zealand.

Austrofusus? crassiaulatus sp. nov.

Fig. 3I-J, M-N

Description. Shell bucciniform of small size (14-22 mm). Protoconch conical of 3½ smooth, slightly swollen whorls, coiled with axis of shell. Teleoconch of five strongly convex, whorls; sutures indented. Spire about half height of shell. Last

whorl slightly concave against posterior suture; contracting abruptly anteriorly and produced into short canal.

Axial sculpture of strong, rounded wide costae, slightly narrower than interspaces, 13 on last whorl; secondary axial sculpture of thin almost lamellate threads over whole shell. Axial sculpture fading rapidly over base of last whorl. Spiral sculpture of well developed lirae much narrower than interspaces present over whole whorl; slightly tuberculate on crossing axial costae; some interspaces with a weaker spiral thread present.

Aperture ovate, produced anteriorly into short strongly twisted anterior canal; interior of outer lip thickened, bearing about eight short lirae. Siphonal notch deep; siphonal fasciole prominent.

Dimensions

Holotype P301912	H 21	W 13	HA 10
Paratype P301913	13	8	6

Type material. Holotype P301912, collected T. A. Darragh, 28 February 1970; Paratype P301913, collected T. A. Darragh, 16 February 1981.

Type locality. PL3001.

Occurrence and material. PL3001 (50 specimens), PL3003 (9 specimens), PL3004 (1 specimen).

Remarks. The genus is known from Middle Eocene to Recent in New Zealand and *Austrofusus* sensu lato from the Late Paleocene of Pitt Island, New Zealand. Many of the New Zealand species have two weak keels. *Austrofusus? crassiaulatus* sp. nov. has only a slight suggestion of a keel at the edge of the shoulder. Of New Zealand taxa, it is most similar to *Austrofusus affiliaus* Finlay, Early Miocene which has one keel more prominent than on *Austrofusus? crassiaulatus*. *A. valedictus* King, Middle-Late Miocene, is somewhat similar but *Austrofusus? crassiaulatus* is much squatter. In its squat shape it has some resemblance to *A. pliocenensis* (Powell), Pliocene. It also has some resemblance to *Pseudofax weddellensis* Stilwell & Zinsmeister, Late Eocene, Antarctica.

Pseudofax Finlay & Marwick, 1937

Type species. *Phos ordinarius* Marshall, 1917, Paleocene, New Zealand.

Pseudofax cf. *ordinarius* (Marshall, 1917)

Fig. 3E-F, K-L

Description. Shell small, of average size for genus (7.5×14.5), elongate-ovate. Protoconch damaged,

of about $2\frac{1}{2}$ smooth convex whorls, coiled in axis of shell. Teleoconch of five whorls. Spire whorls convex, with slightly less convex sutural ramp and weak shoulder. Last whorl contracting abruptly anteriorly and produced into short canal.

Axial sculpture of coarse costae about as wide as interspaces, present from shoulder to anterior suture on spire; on last whorl costae extend to about mid whorl; about 16 on last whorl. Spiral sculpture of strong cords of variable strength, slightly narrower than interspaces, slightly nodulate on crossing axial costae, about 8–12 on spire whorls, slightly more crowded on sutural ramp.

Aperture ovate. Canal short, slightly twisted and notched.

Dimensions

Figured specimen P301914 H 14.5 W 7.5 HA 6.5
Figured specimen P98418 12.5+ 6.5 shell broken

Figured material. Figured specimen P301914, collected T. A. Darragh, 24 November 1992; Figured specimen P98418, collected T. A. Darragh, 16 October 1971.

Occurrence and material. PL3001 (2 specimens).

Remarks. Both specimens are slightly damaged. This taxon is very similar to *Pseudofax ordinarius* (Marshall), but the Pebble Point species has coarser axial costae and finer spiral sculpture. *Pseudofax* is recorded from the Paleocene of New Zealand, the Paleocene of Patagonia and Late Eocene of Antarctica. Somewhat similar taxa occur in the early Tertiary of California under the name of *Molophorus* and in the Paleocene to Oligocene of Europe as *Cominella* eg. *C. deserta* Solander, *C. acies* Walch et and *C. ovata* Deshayes (Stewart 1927) and *C. bicorona* Meville and *Buccinum gossardi* Nyst. *Pseudofax ordinarius* is very similar to *C. bicorona* Meville, Paleocene, Paris Basin. *Pseudofax* may be a synonym of *Molophorus*, but if it is accepted as being sufficiently distinct from the Californian genus or from *Cominella*, the European taxa cited above should be placed in *Pseudofax* because they are so close in morphology to the New Zealand species. Whatever the case, the Southern Hemisphere species belong to a genus with a widespread distribution.

Levifusus Conrad, 1865

Type species. *Fusus trabeatus* Conrad, 1833, Early Eocene, USA.

Levifusus? quadrifunifer sp. nov.

Fig. 3S–U

Description. Shell large (65×84 mm), pyriform of about five whorls with low spire and prominent shoulder on last whorl. Protoconch not well preserved, of one? whorl slightly deviated from axis of shell. Spire whorls enveloped by each succeeding whorl, only flat sutural ramp of spire whorls visible. Last whorl abruptly contracted anterior to anterior spiral cord.

Sculpture on spire whorls of two prominent cords on sutural ramp at posterior and anterior sutures. Last whorl very large with four prominent cords bearing low coarse, somewhat irregular nodules. Posterior cord close to suture, separated from it by four to five fine lirae; second cord at whorl shoulder, 19–20 fine lirae between it and first cord; third cord at mid-whorl, 19–20 fine lirae between it and second cord; fourth cord situated at anterior $\frac{2}{3}$ of whorl. Distance between third and fourth cords smaller than that between second and third cords and with 15 fine lirae present. Interspaces between cords concave. Fine lirae covering entire shell from fourth cord onto anterior canal. Interspaces between fine lirae twice width of lirae.

Aperture wide, polygonal in outline; columella strongly concave; aperture extending anteriorly into a large prominent left twisted canal. Siphonal fasciole well developed.

Dimensions

Holotype P301915 H 84 W 65 HA 50

Type material. Holotype P301915, collected T. A. Darragh, 16 February 1981.

Type locality. PL3001.

Occurrence and material. PL3001 (5 specimens), PL3004 (1 specimen).

Remarks. This taxon belongs with those genera formerly placed in Galeodidae. I follow Ponder & Warén (1988) who reduced this family to a synonym of the subfamily Melongeninae in Buccinidae.

Levifusus is known from the Paleocene and Eocene of the southeastern United States of America. *L. quadrifunifer* is similar to *L. dallianus* Harris, Paleocene of Alabama, but differs in having four prominent spiral cords not two. There do not seem to be any taxa in Europe, New Zealand or Antarctica that are similar to this species. The genus has been recorded from the Paleocene of East and West Africa (Adegoke 1977; Gliozzi &

Malatesta 1985), but the species recorded bear little resemblance to the type species of the genus.

Family FASCIOLARIIDAE

Fusinus Rafinesque, 1815

Type species. *Murex colus* Linnacus, 1758, Recent, Indo-Pacific.

Fusinus sp.

Fig. 4T-U

Description. Shell elongate, fusiform with rounded whorls and long canal. Early spire whorls missing. Whorls regularly convex, slightly depressed at posterior suture.

Spiral sculpture of sharp ridge-like, regularly spaced, weakly denticulate lirae, much narrower than interspaces, seven on penultimate whorl, 11 on last whorl, slightly weaker and more crowded near posterior suture. Canal with seven lirae becoming weaker and fading anteriorly. Transverse sculpture of sinuous growth lines, forming low denticulations on crossing lirae.

Aperture obscured, oval, produced anteriorly into long straight canal.

Dimensions

Figured specimen P301916 H 57 W 20
HA 20 specimen broken

Figured material. Figured specimen P301916, collected T. A. Darragh 16 February 1981.

Occurrence and material. PL3001 (10 specimens), PL3004 (1 specimen) all fragmentary.

Remarks. The most complete fragment consists of the canal, last whorl and about half the penultimate whorl. The other fragments consist of portions of the last whorl and one fragment consisting of the canal only measuring 69 mm in length. There is also a fragment of a spire which is probably the juvenile section of the spire whorls of this species. The youngest two whorls of this specimen have a prominent keel which rapidly decreases in strength abapically so that the whorl profile becomes regularly convex. Weak axial plicae are present, slightly nodulate where they cross the keel. The spiral sculpture consists of about nine regularly and widely spaced, weakly denticulate lirae. The growth lines are similar to the large canaliculate specimen. Until more complete specimens are found, it is not possible to be certain that this spire fragment belongs to the same taxon as the fragments of the last whorls.

This species belongs to a group of narrow aciculate fusiform gastropods present in the early Tertiary. In Australia the previously earliest representative of the group was *Fusinus sculptilis* (Tate), Late Eocene of Victoria and South Australia. There is also a species similar to the Pebble Point species in the Early Miocene of Tasmania and Tasmania in which the spire whorls bear prominent axial costae which become weaker anteriorly and eventually disappear except for slight denticulations on the spiral lirae. It also has a very weak, slightly dentate keel on the earliest spire whorls. These species are probably ancestral to the late Tertiary to Recent, *Fusinus novae-hollandiae*.

The Pebble Point species is somewhat similar to *Fusinus dissimilis* (Deshayes, 1865), Late Eocene, Paris Basin, but the former has more rounded whorls and more regular and equal lirae than *F. dissimilis*. *F. aciculatus* Lamarck, Eocene, Paris Basin does not have keeled juvenile whorls.

Family TURBINELLIDAE

Columbarium Martens, 1881

Type species. *Pleurotoma (Columbarium) spinicincta* Martens, 1881, Recent, Queensland.

Columbarium rugatoides sp. nov.

Fig. 4L-M

Description. Shell of average size for genus, fusiform with gradate spire of about six prominently shouldered whorls. Protoconch large, of 1½ smooth whorls; first whorl globular, deviated at right angles to axis of shell. Spire whorls with posterior whorl slope smooth, flat to slightly concave. Shoulder forming prominent keel bearing triangular spikes. Anterior whorl slope with one lira at about mid point, and one stronger cord with prominent scales or triangular spikes against anterior suture of all spire whorls, becoming stronger adaperturally. Last whorl with prominent spinose cord at anterior 2/3, anterior to this a slightly less well developed anterior carina and another lira between anterior carina and canal.

Aperture subquadrate, continuous, notched posteriorly; columella covered with curved plate; outer lip slightly produced and toothed where intersected by anterior carina. Canal straight, bearing well developed thin, widely spaced spinose lirae.

Dimensions

Holotype P301917 H 35 broken W 15.5 HA 7.5

Type material. Holotype P301917, collected T. A. Darragh, 19 November 1970.

Type locality. PL3004.

Occurrence and material. PL3001 (2 specimens), PL3003 (1 specimen), PL3004 (1 specimen).

Remarks. In its sculpture *Columbarium rugatoides* sp. nov. resembles *C. spinicinctum* and in shape it is somewhat similar to *C. rugatum* (Aldrich, 1886), Early Eocene, Alabama. *C. rugatoides* sp. nov. is probably ancestral to *C. calcaratum* Darragh, 1969, Late Eocene–Early Oligocene, Victoria, but it is more elongate and not as spinose, the whorls are more quadrate in outline and it has less spiral cords on the anterior part of the body whorl. In sculpture *C. rugatoides* is somewhat similar to *C. vulneratum* (Finlay & Marwick), Paleocene, New Zealand, but the whorls are more quadrate in outline.

Columbarium has a cosmopolitan distribution in the Paleocene, occurring in Europe, Ukraine (Makarenko 1976), United States of America and New Zealand (Darragh 1969, 1987).

Microfulgur Finlay & Marwick, 1937

Type species. *Latirus (Mazzalina) longirostris* Marshall, 1917, Paleocene, New Zealand.

Microfulgur ? sp.

Fig. 4J–K

Description. Shell small, biconical, fusiform. Protoconch missing. Teleoconch whorls 4+. Spire whorls with prominent flat sutural ramp making up $\frac{2}{3}$ of exposed spire whorl. Ramp with prominent lirae. Last whorl very convex anterior to ramp and then contracting rapidly to anterior canal.

Spiral sculpture of well developed lirae, much narrower than interspaces, five lirae on ramp of last whorl, three stronger lirae on remainder of last whorl, of which shoulder lirate and two anterior to it are strongest.

Aperture oval. Columella with anterior fold or twist. Canal broken.

Dimensions

Figured specimen P301918 H 10 canal broken W 7.5

Figured material. Figured specimen P301918, collected T. A. Darragh & K. Bell, 21 November 1970.

Occurrence and material. PL3001 (1 specimen).

Remarks. The single specimen is broken and partly decorticated, so a precise description is not possible.

This species is placed in *Microfulgur* with some hesitation. Compared with *M. longirostris* (Marshall), the Pebble Point species is wider with a sharp shoulder and fewer spiral lirae. *Microfulgur* is known with certainty only from the Paleocene of New Zealand. The Pebble Point taxon bears some resemblance to *Strepsidura luciani* (Briart & Cornet, 1870) as figured by Makarenko (1976) from the Paleocene of Ukraine, but does not have the twisted canal of that taxon.

Family MITRIDAE

Mitra Lamarck, 1798

Type species. *Voluta mitra* Linnaeus, 1758, Recent, Indo-Pacific.

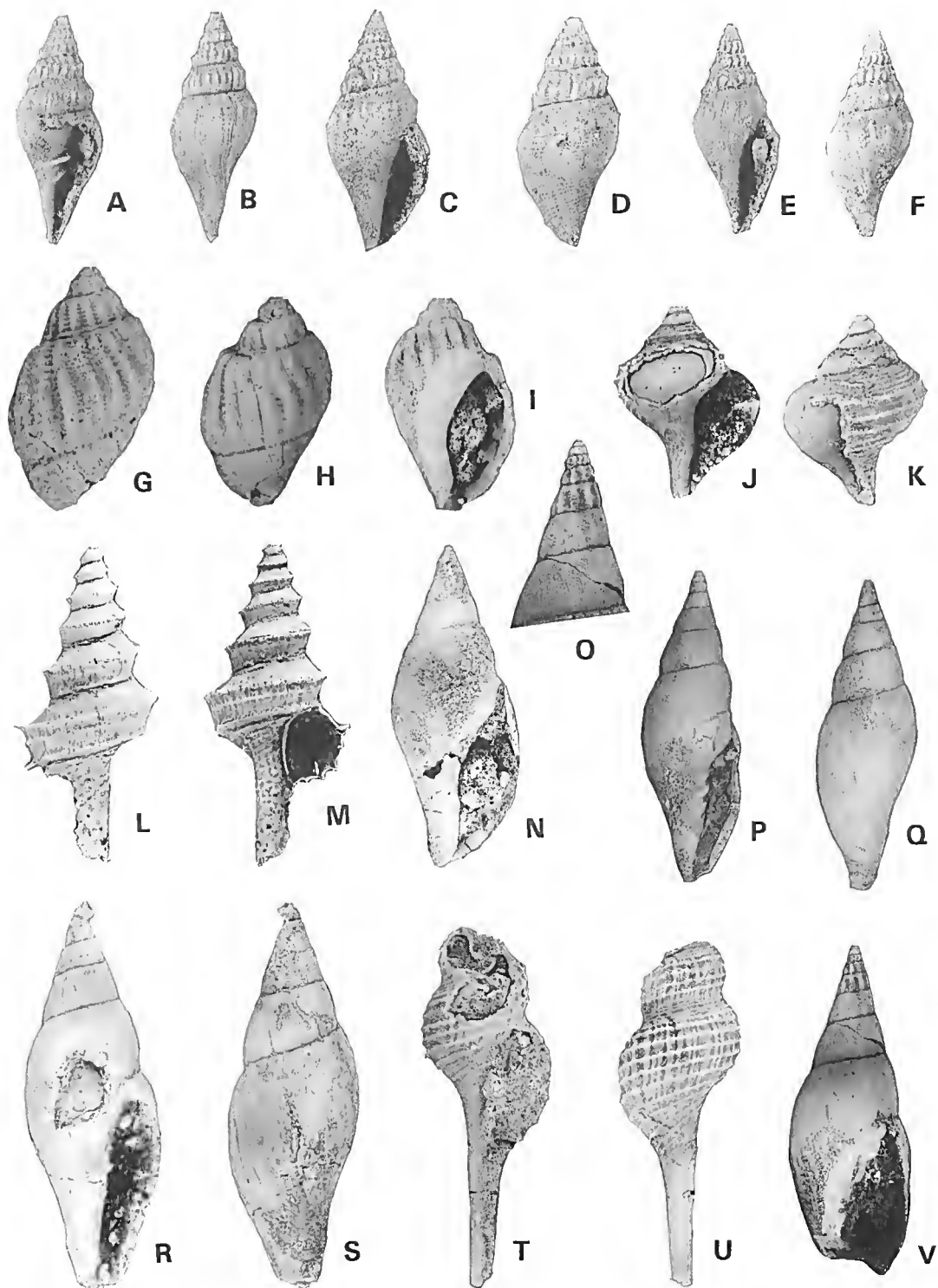
Mitra? rhytidata sp. nov.

Fig. 4N–S, V

Description. Shell of medium size for genus (16×47–20×49 mm), elongate fusiform with subconical spire and gently tapering last whorl. Protoconch of about $3\frac{1}{4}$ smooth regularly convex whorls, first whorl deviated about 30° from axis of shell, sutures impressed. Spire whorls flat to slightly convex.

Spiral sculpture of close threads covering whole of whorl, becoming indistinct on last whorl. Axial sculpture of well developed sharp plicae, extending from suture to suture, beginning on first

Fig. 4. A–F, *Proximitra trirugulata* sp. nov., NMV P301923, holotype, PL3001, A, ×2.5, B, ×2.3. C–D, NMV P301924, paratype, PL3001, ×3.0. E–F, NMV P11829, paratype, PL3001, ×3.0. G–I, *Pseudoliva (Buccinorbis)* sp. G, NMV P301925, figured specimen, PL3001, ×1.3. H–I, NMV P301926, figured specimen, PL3001, ×1.3. J–K, *Microfulgur?* sp., NMV P301918, figured specimen, PL3001, ×2.9. L–M, *Columbarium rugatoides* sp. nov., NMV P301917, holotype, PL3004, ×1.4. N–S, V, *Mitra? rhytidata* sp. nov., NMV P301919, paratype, PL3001, ×1.0. O–V, NMV P301922, paratype, PL3001, O, ×1.5, V, ×1.0. P–Q, NMV P301921, holotype, PL3001, ×1.0. R–S, NMV P301920, paratype, PL3001, ×1.0. T–U, *Fusinus* sp., NMV P301916, figured specimen, PL3001, ×0.9.



teleoconch whorl and present on second to third whorl then fading rapidly, 11–12 on first whorl, 10 on second whorl, about 9 on third whorl on some specimens.

Aperture narrowly elongate; outer lip slightly thickened, produced anteriorly into short canal; siphonal notch well developed; siphonal fasciole moderately developed; columella covered with thin callus, bearing two strong central plaits flanked by two slightly weaker plaits.

Dimensions

Holotype P301921	H 47	W 16	HA 24
Paratype P301919	49	20	28
Paratype P301920	60	21	29
Paratype P301922	49	19	specimen broken

Type material. Holotype P301921, collected T. A. Darragh, 21 November 1970; Paratype P301919, collected T. A. Darragh & D. J. Holloway, 24 November 1992; Paratype P301920, collected A. G. Beu, 16 October 1971; Paratype P301922, collected T. A. Darragh, 14 December 1994.

Type locality. PL3001.

Occurrence and material. PL3001 (9 reasonably complete and 12 fragmentary specimens), PL3003 (5 fragmentary specimens).

Remarks. This species is unusual for a mitrid in having two strong central plaits and a weaker posterior and anterior plait and in having plicae on the juvenile teleoconch whorls. The plicate spire may suggest a costate ancestor such as *Mesorhytis*. Large species of *Mitra* are rare in the Paleocene and none seem to be related to this taxon. *M.?* *rhytidata* sp. nov. looks a little like *Mitra elongata* Lamarck, Eocene, Paris Basin in shape but that species lacks axial or spiral sculpture. There is nothing quite like it in the Eocene or later Tertiary of Australia. *M.?* *rhytidata* is more tumid and the spire not nearly so elongate as *Eumitra alokiza* Tenison Woods and *E. uniplica* Tate, Miocene, Victoria.

Family VOLUTOMITRIDAE

Proximitra Finlay, 1926

Type species. *Vexillum (Costellaria) rutidolomum* Suter, 1917, Early Miocene, New Zealand.

Proximitra trirugulata sp. nov.

Fig. 4A–F

Description. Shell of medium size for genus, fusiform with slightly shouldered whorls. Proto-

conch of two smooth whorls, the first swollen and deviated at about 45° to spire axis. Teleoconch whorls five, with weak shoulder developing on first whorl; shoulder slightly convex at suture, then concave. Shoulder angulation on spire slightly anterior of mid whorl. Last whorl tapering gently anteriorly.

Axial sculpture of coarse costae, very weak on sutural ramp, extending to anterior suture on spire, becoming obsolete or confined to shoulder angulation on last whorl, 20 costae on penultimate whorl. Spiral sculpture of flat, well developed lirae about as wide as interspaces present over whole whorl. Aperture long, narrow, produced into very short canal. Columella with two strong anterior plaits and one weaker posterior plait. No siphonal fasciole.

Dimensions

Holotype P301923	H 15	W 5.5	HA 7
Paratype P118292	10.5	4.5	5
Paratype P301924	12	5.2	6

Type material. Holotype P301923, collected T. A. Darragh, 21 November 1970; Paratype P118292, collected T. A. Darragh, 16 February 1981; Paratype P301924, collected T. A. Darragh & K. Bell, 28 February 1970.

Type locality. PL3001.

Occurrence and material. PL3001 (18 specimens), PL3003 (2 specimens).

Remarks. The genus occurs in New Zealand from Middle Eocene to Early Pliocene, in France in the Eocene, in the United States of America in the Miocene, and in Australia from Early to Mid Miocene (Cernohorsky 1970). If the generic assignment is correct, the range of the genus is now extended back to the Paleocene. The specimens figured by Kollmann and Peel (1983, fig. 226) as *Cordieria* from the Paleocene of Greenland are very similar to *Proximitra trirugulata* sp. nov. but are more elongate. *P. trirugulata* has some resemblance New Zealand species, particularly to *P. parki* (Allan 1926), Late Eocene, New Zealand (Maxwell 1992), but differs by being more slender and having more prominent axial sculpture and fine spiral lirae over the whole shell. It bears little resemblance to the Australian Miocene species.

Family OLIVIDAE

Pseudoliva (Buccinorbis) Conrad, 1867

Type species. *Monoceras vetusta* Conrad, 1833, Eocene, United States of America.

Pseudoliva (*Buccinorbis*) sp.

Fig. 4G-I

Description. Shell solid, of average size for genus (16x28 mm), roundly fusiform, slightly ventricose with subconical spire about $\frac{1}{3}$ height of shell. Protoconch not preserved. Spire whorls four. Whorls gently convex, suture impressed to slightly channelled.

Axial sculpture of prominent coarse, slightly sigmoidal costae, slightly narrower than interspaces, about 17 per whorl. Spiral sculpture of well developed lirae about as thick as interspaces, eight to nine on penultimate whorl. Last whorl regularly convex, tapering slightly anteriorly, with prominent spiral groove at anterior third, covered with well developed lirae, 16-17 lirae posterior to groove and about nine anterior to groove.

Aperture regularly lenticular with very short, wide anterior canal. Inner lip with prominent callus. Siphonal fasciole moderately developed.

Dimensions

Figured specimen P301925	H 28	W 16	HA 17
Figured specimen P301926	24	15	15

Figured material. Figured specimen P301925, collected T. A. Darragh & D. J. Holloway, 24 November 1992; Figured specimen P301926, collected K. Bell & T. A. Darragh, 23 November 1970.

Occurrence and material. PL3001 (2 specimens).

Remarks. This species belongs to a group of axially sculptured species present in the Late Cretaceous to Paleocene of France, Belgium, Germany, Copenhagen, Ukraine, Greenland, India and United States of America for which the generic taxa *Pseudoliva* and *Buccinorbis* have been variously used (Adegoke 1977). Species of *Buccinorbis* differ from those of *Pseudoliva* by the presence of strong axial and spiral sculpture and the genus is used for such sculptured European, Indian and American species.

The Pebble Point species is very similar to *B. curvicostata* (Briart & Cornet, 1870), Paleocene, Belgium, but is not so squat. *B. koeneni* Ravn, 1939, Paleocene, Copenhagen, is a small species not so globose as that from Pebble Point and with less prominent axials. There are no records of the genus from the Paleocene of New Zealand or the Late Eocene of Antarctica. The genus does not occur above the Paleocene in Australia. It may, however, be ancestral to the Australian endemic genus, *Zemira*, which ranges in age from Early Oligocene to Recent. The earliest occurrence of *Zemira* is an undescribed species from the Early

Oligocene of Point Flinders, Victoria (Ponder & Darragh 1975) which has an umbilicus like many species of *Buccinorbis* but lacks the prominent axial sculpture of the latter genus.

Family TURRIDAE

Zemacies Finlay, 1926

Type species. *Zemacies elatior* Finlay, 1926, Miocene, New Zealand.

Zemacies procerior sp. nov.

Fig. 50-P, U

Description. Shell of average size for genus (31 mm), elongate, fusiform, spire about $\frac{2}{3}$ height of shell. Protoconch conical, of four smooth whorls, coiled with axis of shell. Teleoconch of about 7 whorls with concave ramp and blunt shoulder. Last whorl tapering gently to long anterior canal.

Axial sculpture of low broad opisthoelone costae on shoulder (about 16 present) and extending to anterior suture on first four teleoconch whorls, on subsequent whorls becoming weaker and obsolete on last two whorls. Spiral sculpture of fine weak closely spaced lirae over whole whorl.

Aperture long and narrow; outer lip with deep notch on ramp. Columella long, straight and covered with thin glaze of callus.

Dimensions

Figured specimen P98421	H 31	W 9	HA 13.5
Figured specimen P98419	11.2	4.5	5

Figured material. Figured specimen P98421, collected K. N. Bell & T. A. Darragh, 28 February 1970; Figured specimen P98419, collected T. A. Darragh, 16 October 1971.

Occurrence and material. PL3001 (6 specimens).

Remarks. There are three other specimens which may belong to this taxon, but are too weathered for precise determination. Of the other six only one is a mature specimen. *Zemacies* in New Zealand ranges from Paleocene to Early Pliocene. In Australia it is known only from the Late Oligocene (*Z. inexpectata* Powell, 1944). *Apiotoma*, which ranges from Late Eocene to Mid Miocene, is somewhat similar in shape and sculpture to *Zemacies* but has a paucispiral protoconch. However, Bouchet (1990) has pointed out that such differences in turrid protoconchs do not have generic significance, so that *Zemacies* may well be a synonym of *Apiotoma*.

This taxon is very similar to *Zemacies immatura* Finlay & Marwick, 1937, Paleocene, New Zealand, but *Z. procerior* is relatively more elongate and without the infra-sutural cord present on *Z. immatura*. *Z. procerior* is very similar to the type species of the genus *Z. elatior*, but has more prominent axial costae present on about half the spire whorls and lacks the subsutural cord present in *Z. elatior*.

Stilwell & Zinsmeister (1992) record *Zemacies* from the Late Eocene of Antarctica but the specimens lack protoconchs and look more like *Apiotoma*.

Cosmasyrinx (*Tholitoma*)

Finlay & Marwick, 1937

Type species. *Tholitoma dolorosa* Finlay & Marwick, 1937, Paleocene, New Zealand.

I follow Maxwell (1992) who reduced *Tholitoma* to a subgenus of *Cosmasyrinx* Marwick, 1931.

Cosmasyrinx (*Tholitoma*) *levicristata* sp. nov.

Fig. 5R, V–W, Z

Description. Shell of medium size for genus (9–11.5 mm), elongate, pagodiform, with sharply angulate whorls. Protoconch of $4\frac{1}{2}$ convex whorls coiled in axis of shell; first $3\frac{1}{2}$ whorls smooth, next whorl bearing fine curved opisthocline axial ribs, concave adaperturally. Teleoconch whorls three with prominent flat to convex ramp and well developed shoulder slightly anterior to mid whorl on spire whorls.

Axial sculpture of obscure opisthocline elongate tubercles restricted to shoulder flange. Spiral sculpture of fine closely spaced threads present over whole shell with one coarser thread bearing prosocline nodules close to posterior suture.

Aperture triangular, outer lip with deep sinus on ramp. Columella long and straight.

Dimension

Holotype P301930	L 8.8	W 4.4	HA 4.4
Paratype P98415	10	5	5

Type material. Holotype P301930, collected T. A. Darragh, 24 November 1992; Paratype P98415, collected T. A. Darragh, 16 October 1971.

Type locality. PL3001.

Occurrence and material. PL3001 (8 specimens), PL3003 (5 specimens).

Remarks. *Cosmasyrinx* (*Tholitoma*) *levicristata* sp. nov. differs from *C. (T.) dolorosa* by its less prominent sculpture and more prominent keel. It has some resemblance to species of the genus *Cochlespira* but it is relatively smoother, has a weakly tuberculate shoulder rather than the serrate shoulder of many species in the genus, and the ramp is flat to convex rather than flat to concave as in most species of *Cochlespira*.

The subgenus is known from the Paleocene and Eocene of New Zealand. A somewhat similar species, *Cosmasyrinx brychiosinus* Stilwell & Zinsmeister, occurs in the Late Eocene of Antarctica.

Marshallaria Finlay & Marwick, 1937

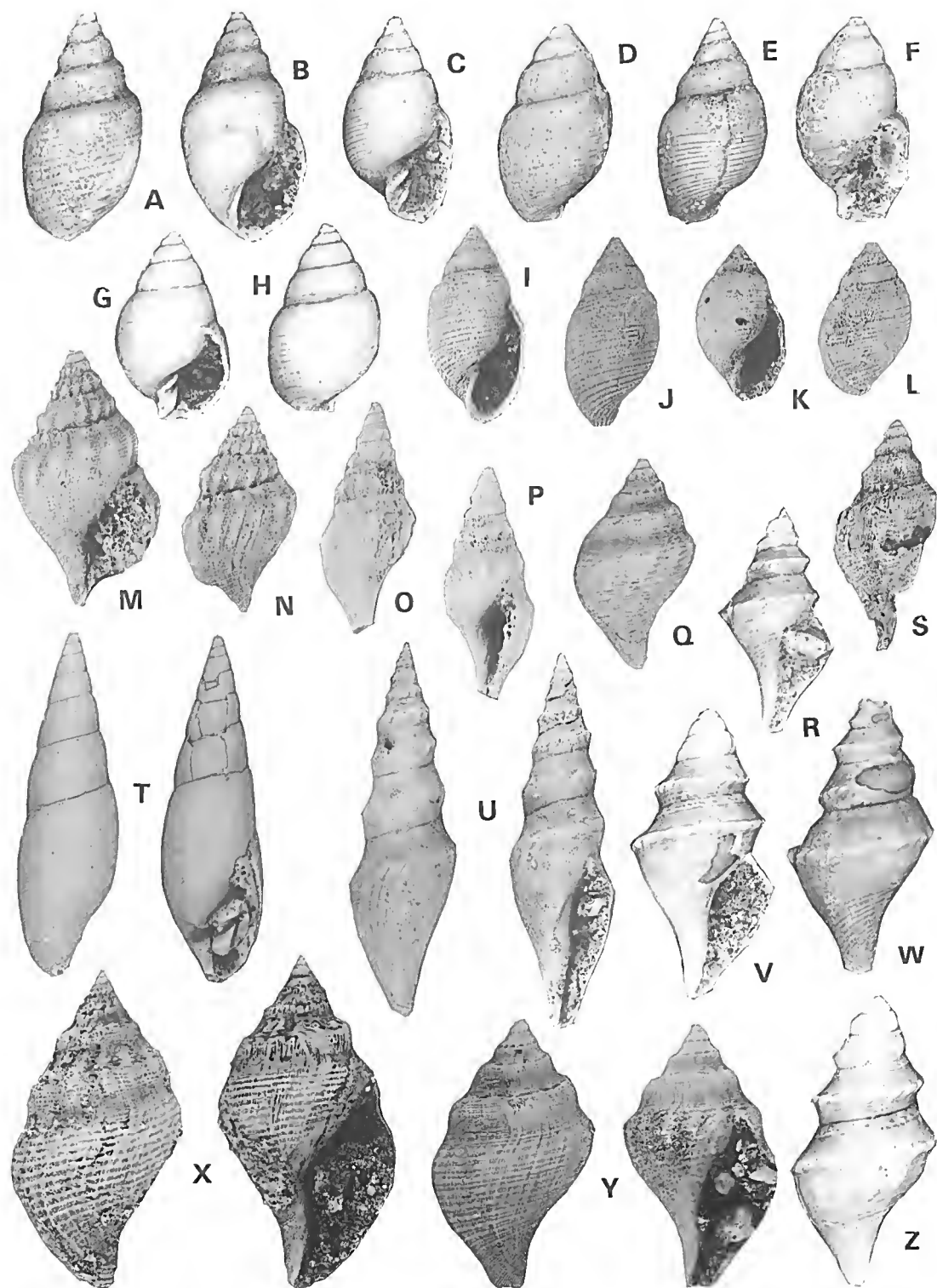
Type species. *Verconella spiralis* Allan, 1926, Late Eocene, New Zealand.

Marshallaria tumefacta sp. nov.

Fig. 5Q, X–Y

Description. Shell of average size for genus (height 22–30+ mm), biconic, squat, tumid at mid whorl and tapering rapidly anteriorly. Protoconch of about $2\frac{1}{2}$ smooth rounded whorls. Teleoconch of four to five whorls; spire about $\frac{1}{3}$ shell height. First teleoconch whorl regularly convex bearing fine spiral threads on first half whorl; last half whorl with axial costae extending from suture

Fig. 5. A–B, *Acteon* sp. b, NMV P301966, figured specimen, PL3001, $\times 5.0$. C–H, *Tornatellaea quindecimlirata* sp. nov. C, E, NMV P301967, holotype, PL3004, $\times 3.8$. D, F, NMV P301968, paratype, PL3001, $\times 4.1$. G–H, NMV P118290, paratype, PL3001, $\times 4.1$. I–L, *Acteon petricolus* sp. nov. I–J, NMV P301931, holotype, PL3003, $\times 3.0$. K–L, NMV P301932, paratype, PL3003, $\times 2.9$. M–N, *Marshallaria* sp. a, NMV P301964, figured specimen, PL3001, M, $\times 3.0$, N, $\times 2.3$. O–P, U, *Zemacies procerior* sp. nov. O–P, NMV P98419, figured specimen, PL3001, $\times 3.1$. U, NMV P98421, figured specimen, PL3001, $\times 1.8$. Q, X–Y, *Marshallaria tumefacta* sp. nov. Q, NMV P301929, paratype, PL3001, $\times 1.8$. X, NMV P301928, paratype, PL3003, $\times 1.8$. Y, NMV P301927, holotype, PL3001, $\times 1.8$. R, V–W, Z, *Cosmasyrinx* (*Tholitoma*) *levicristata* sp. nov. R, W, NMV P98415, paratype, PL3001, R, $\times 4.1$, W, $\times 3.2$. V, Z, NMV P301930, holotype, PL3001, $\times 4.9$. S, *Marshallaria* sp. b, NMV P301965, figured specimen, PL3003, $\times 2.4$. T, *Tenuiacteon* sp., NMV P302273, figured specimen, PL3001, $\times 3.0$.



to suture. Remainder of teleoconch whorls with prominent shoulder and ramp. Ramp convex against posterior suture forming well developed subsutural fold and deeply concave anterior to this. Spire whorls anterior to shoulder completely enveloped by each succeeding whorl.

Axial sculpture apart from first teleoconch whorl consisting of tubercles on shoulder, exposed on second and third teleoconch whorl, partly covered by succeeding whorls and becoming obsolete on last whorl. Spiral sculpture of strong cords, finer on ramp and coarser on last whorl anterior to shoulder, with fine threads in interspaces.

Aperture long, narrow, produced anteriorly into short canal; sinus arcuate, very broad, shallow, apex in middle of ramp; columella covered with thin callus; siphonal notch weak; no siphonal fasciole.

Dimensions

Holotype P301927	H 22	W 13	HA 15
Paratype P301928	26.5	14	16
Paratype P301929	17.5	9.5	11

Type material. Holotype P301927, collected T. A. Darragh, 21 November 1970; Paratype P301928, collected T. A. Darragh, 13 November 1984; Paratype P301929, collected T. A. Darragh, 14 December 1994.

Type locality. PL3001.

Occurrence and material. PL3001 (26 specimens), PL3003 (2 specimens), PL3004 (4 specimens), PL3005 (1 specimen).

Remarks. The genus is known only from New Zealand and southeastern Australia. In New Zealand it ranges in age from Early Paleocene to Late Miocene. In Australia *Marshallaria* has been recorded previously only from the Early Oligocene. *M. tunefacta* is not particularly close to any of the described species. It bears some similarity to *M. multicincta* Marshall, Paleocene, New Zealand, but is far more tumid and the spire whorls are enveloped by the succeeding whorls. It is somewhat similar to the species figured as *Turricula* by Kollmann & Peel (1983) from the Paleocene of Greenland and it is also similar to *Austrotoma ventricosa* Stilwell & Zinsmeister, 1992, Late Eocene, Antarctica, but *M. tunefacta* is more tumid and the shoulder tubercles are more prominent.

Marshallaria sp. a

Fig. 5M–N

Description. Shell of average size for genus (13 mm), broadly fusiform, with somewhat gradate

spire less than half height of shell. Protoconch of three to four regularly convex whorls coiled in axis of shell, first two to three whorls smooth, last whorl with about seven broad lirae, wider than interspaces. Teleoconch of four whorls with prominent rounded shoulder; sutural ramp concave, bounded against posterior suture by one broad cord. Last whorl abruptly contracted anteriorly to form short canal.

Spiral sculpture continuing from protoconch, covering whole of last whorl, 37+ on last whorl, somewhat granulated where crossed by coarse growth lines. Axial sculpture of coarse costae, beginning as narrow plicae on first teleoconch whorl and rapidly increasing in strength, 15 on last whorl, strongest at shoulder and stronger on subsutural cord, extending to anterior suture on spire whorls, fading rapidly anteriorly on last whorl.

Aperture subtriangular; outer lip with shallow broad sinus on ramp; inner lip with thin callus. Canal short, narrow, without notch; siphonal fasciole very weak.

Dimensions

Figured specimen P301964 H 13 W 7 HA 6.5

Figured material. Figured specimen P301964, collected T. A. Darragh, 24 November 1992.

Occurrence and material. PL3001 (1 specimen), PL3009 (1 specimen).

Remarks. The specimen from PL3009, Dilwyn Formation, of Early Eocene age is a juvenile but seems to be the same species as that from the Pebble Point Formation. The Pebble Point taxon is somewhat similar to *Marshallaria decipiens* Maxwell, 1992, Eocene, New Zealand but is more tumid and the spiral sculpture is much finer than that species. The Pebble Point species has more prominent sculpture than *M. multicincta* (Marshall, 1917), Paleocene, New Zealand. *M. otwayensis* Long, 1981, Early Oligocene, Victoria, has much weaker sculpture and a more twisted columella.

Marshallaria sp. b

Fig. 5S

Description. Shell of medium size for genus (6×14.5 mm), fusiform with gradate spire; spire about one third height of shell. Protoconch damaged or missing, of 3½ convex whorls, first two (?) smooth, last whorl with seven prominent lirae. Teleoconch of three whorls with prominent shoulder; sutural ramp sloping, flat. Last whorl tapering abruptly to form moderately long canal.

Spiral sculpture of prominent, closely spaced granulated cords; 11 on spire whorls, 28+ on last whorl. Axial sculpture of growth lines only.

Aperture damaged; outer lip with shallow broad sinus.

Dimensions

Figured specimen P301965 W 6 H 14.5 HA 8.5

Figured material. Figured specimen P301965, collected T. A. Darragh, 13 November 1984.

Occurrence and material. PL3001 (1 specimen), PL3003 (1 specimen).

Remarks. This species is distinguished from *Marshallaria* sp. a by the absence of axial sculpture. It is also much more slender. The protoconch is almost identical in morphology, so far as can be judged on the available material. It is somewhat similar to *M. multicincta* (Marshall, 1917), Paleocene, New Zealand, but it has a flat rather than concave sutural ramp and lacks any axial sculpture.

Family ACTEONIDAE

Acteon Montfort, 1810

Type species. *Voluta tornatilis* Linnaeus, 1767, Recent, Europe.

Acteon petricolus sp. nov.

Fig. 51-L

Description. Shell small (5×9.5 mm), subfusiform to ovate; spire about one third height of shell. Protoconch of one smooth whorl; first half whorl swollen, deviated at 45° to axis of shell. Teleoconch whorls 3½. Spire whorls regularly convex; sutures impressed.

Sculpture of wide spiral grooves, slightly narrower than interspaces; grooves interrupted at regular intervals by thin axial septa, so that groove consists of a series of rectangles; six grooves on spire whorls; last whorl covered with about 22 grooves.

Aperture lenticular; outer lip regularly and gently convex, slightly produced anteriorly. Columella covered with thin glaze, bearing one prominent fold where joined by outer lip, deep rounded channel posterior to fold.

Dimension

Holotype P301931	H 9.5	W 5	HA 5
Paratype P301932	8	4	4

Type material. Holotype P301931, Paratype P301932, collected T. A. Darragh, 18 November 1984.

Type locality. PL3003.

Occurrence and material. PL3003 (6 specimens).

Remarks. Species of *Acteon* are very widely distributed in the Paleocene. *A. petricolus* sp. nov. has some resemblance to *A. semispiralis* Marshall, 1917, Paleocene, New Zealand, but is more elongate and the spire whorls are more regularly rounded and the suture is impressed. Species of *Acteon* are known in the Tertiary of southern Australia from Eocene to Recent. *A. petricolus* has very little resemblance to the Eocene species. It is much larger, not so tumid and has flatter and more cylindrical whorls than *A. evanescens* Cossmann, 1897 from the late Eocene of southern Australia. *A. petricolus* is very similar to *Acteon scrobiculatus* Tenison Woods, 1877, Late Oligocene–Early Miocene, but has finer sculpture and a slight suggestion of a shoulder which is lacking in *A. scrobiculatus*. The spire is also not so tapering and the last whorl is more cylindrical than in *A. scrobiculatus*.

Acteon sp. b

Fig. 5A–B

Description. Shell small (5×9.5 mm), elongate-ovate with gradate spire. Protoconch heterostrophic of 2½ smooth whorls, first two whorls deviated at 137° to axis of shell, partly immersed. Whorls with prominent rounded shoulder, flat anterior to shoulder, sutures impressed, slightly channelled.

Sculpture of widely spaced grooves with transverse bars, more crowded on shoulder, 10–11 on spire whorls, about 22–27 on last whorl.

Aperture about half height of shell, narrowly elliptical. Columella covered with weak callus bearing one weak fold.

Dimension

Figured specimen P301966	H 7	W 3.5	HA 3.5
Measured specimen P302641	9.5	5	5.5

Figured material. Figured specimen P301966, collected T. A. Darragh, 28 February 1970.

Occurrence and material. PL3001 (3 specimens), PL3003 (4 specimens).

Remarks. *Acteon* sp. b is closest to *A. semispiralis* Marshall, 1917, Paleocene, New Zealand, but it has spiral grooves present over the entire whorl, the whorls are not so convex and the spire is gradate. Compared to the Pebble Point species, *A. semispiralis* has a gradate spire and the columella has only a very weak fold. The Pebble Point species has some resemblance to the Paris

Basin Eocene species *A. subinflatus* d'Orbigny, 1850 and *A. turgidus* (Deshayes, 1862) but has a more gradate spire and the whorls are not so convex as these. The prominent gradate spire of this species separates it from all other Australian Tertiary species.

Tenuiactaeon Aldrich 1921

Type species. *Tenuiactaeon pertenuis* Aldrich 1921, Eocene, United States of America.

Tenuiactaeon sp.

Fig. 5T

Description. Shell lanceolate, of six rather flat whorls; whorls somewhat imbricated, sutures impressed. Protoconch deviated at right angles to axis of shell (heterostrophic). Sculpture of widely spaced fine grooves, covering whole whorl, becoming wider and more irregularly spaced on anterior portion of last whorl.

Aperture elongate, lenticular. Columella with one wide fold, interior of aperture obscured with matrix.

Dimensions

Figured specimen P302273 L 17.1 HA 6.5 W 4.9

Figured material. Figured specimen P302273, collected T. A. Darragh, 17 January 1996.

Occurrence and material. PL3001 (one specimen).

Remarks. The aperture of the single specimen is filled with hard matrix and attempts to clear it damaged the columella, so it is not possible to determine the strength of the fold on the columella. This species has some similarity to species of *Nonacteonina* Stephenson, 1941, late Cretaceous, United States of America. Hitherto *Tenuiactaeon* has not been recorded from outside the United States of America.

This species is very similar to *T. olivellaeformis* (Tate), Late Oligocene–Middle Miocene, Victoria, but is somewhat larger (largest Muddy Creek Formation specimen of *T. olivellaeformis* is 14 mm in length) and also differs in having coarser grooves which are regularly spaced over the whole of the whorls. These tend to be irregularly spaced in *T. olivellaeformis*.

Tornatellaea Conrad, 1860

Type species. *Tornatellaea bella* Conrad, 1860, Eocene, United States of America.

Tornatellaea quindecimilirata sp. nov.

Fig. 5C–H

Description. Shell small, of average size for genus (5×7.7 mm), elongate, subcylindrical, with gradate spire. Protoconch of one smooth whorl, tip immersed, slightly deviated from axis of shell. Teleoconch of four whorls, convex only at shoulder. Sutures impressed.

Sculpture of well spaced punctate grooves, absent near the shoulder on some specimens, 15 on last whorl, slightly crowded anteriorly.

Aperture lenticular. Columella with two, thin high plaits.

Dimensions

Holotype P301967	H 8	W 4.5	HA 3.6
Paratype P118290	7	4	3
Paratype P301968	7.5	5	3.5

Type material. Holotype P301967, collected T. A. Darragh, 13 December 1994; Paratype P118290, collected T. A. Darragh, 16 February 1981; Paratype P301968, collected T. A. Darragh, 21 November 1970.

Type locality. PL3004.

Occurrence and material. PL3001 (15 specimens), PL3003 (39 specimens), PL3004 (5 specimens).

Remarks. *Tornatellaea quindecimilirata* sp. nov. is somewhat similar to *T. morbosa* Finlay & Marwick, 1937, Paleocene, New Zealand, but is much more tumid. It has a much more sharply defined shoulder when compared with *T. saucia* Finlay & Marwick, 1937, Paleocene, New Zealand. *Tornatellaea* has a cosmopolitan distribution in the Paleocene. The genus has hitherto not been recorded from Australia. In New Zealand the genus is also known only from the Paleocene.

Family RINGICULIDAE

Gilbertina Morlet, 1888

Type species. *Gilbertina inopinata* Morlet, 1888, Paleocene, France.

Gilbertina meridiana sp. nov.

Fig. 6A–F, H–I

Description. Shell small, of average size for genus (4×4 mm), solid, subglobular of 3½ whorls, spire barely projecting. Protoconch of 1½ smooth whorls coiled at slight angle to axis of shell

and sunken below spire whorls. Spire of 2-2½ rounded whorls. Last whorl large, uniformly inflated, almost covering penultimate whorl.

Sculpture of widely spaced spiral, punctate grooves more crowded towards posterior suture; nine spirals on spire whorls, 16-19 on last whorl.

Aperture pyriform; outer lip thickened into varix, interior of outer lip bearing one small ill defined denticle on some specimens. Siphonal notch shallow, broad, situated to right of midline of aperture. Columella covered with thick callus, bearing two blade-like plaits; thick vertical ridge of callus present posterior to plaits on dorsal part of columella.

Dimension

Holotype P301969	H 5.2	W 4.7	HA 3.1
Paratype P301970	4.0	3.8	2.7
Paratype P301971	4.2	3.8	2.2
Paratype P301972	4.7	4.3	2.8

Type material. Holotype P301969, Paratype P301970, collected T. A. Darragh, 24 November 1992; Paratype P301971, collected T. A. Darragh, 13 November 1984; Paratype P301972, collected T. A. Darragh, 23 November 1992. Paratype WAM 94.410, collected G. W. Kendrick, 13 November 1984.

Type locality. PL3003.

Occurrence. PL3001 (6 specimens), PL3003 (79 specimens), PL3004 (9 specimens).

Remarks. Three specimens have gastropod boreholes on the dorsal side of the last whorl. Species of the genus are found in Paleocene strata of Greenland, Denmark, Poland, France, Austria, Texas, Alabama and California, but it has not been recorded before in the Southern Hemisphere. *Gilbertina meridiana* sp. nov. is most similar to *G. ultima* (von Koenen, 1885), Paleocene, Copenhagen, but differs by the presence of a strong ridge of callus on the edge of the columella.

In the overlying Riverbank Member of the Dilwyn Formation there is another superficially similar species. It is much larger, has four plaits on the columella, and complex denticles on the inner side of the outer lip. It seems to belong to *Superstes* Finlay & Marwick, known from Paleocene to Eocene of New Zealand, and is described and figured for comparison with the Pebble Point Formation taxon.

Superstes Finlay & Marwick, 1937

Type species. *Superstes phoenix* Finlay & Marwick, 1937, Late Eocene, New Zealand.

Superstes glomerabilis sp. nov.

Fig. 6J-O

Description. Shell of average size for genus (7×5.5-8.5×7 mm), subglobular, of three to four whorls, spire scarcely projecting. Protoconch of two smooth whorls, first whorl sunken and slightly deviated from shell axis. First teleoconch whorl sculptured with punctate grooves, later whorls on some specimens smooth, others sculptured with punctate grooves present over whole whorl or confined to anterior quarter of last whorl.

Aperture pyriform with prominent shallow anterior notch. Outer lip slightly prosocline, considerably thickened, bearing fine denticulations on inner side and one prominent denticle at anterior 2/3; on some specimens a second denticle at about mid point of outer lip.

Columella covered with thick callus, strongly curved, with prominent thin vertical ridge between posterior of central plaits and posterior end of aperture. Four plaits; two strong, central, blade-like plaits; a third strong plait posterior to these set well into aperture behind vertical ridge and one weaker anterior, almost vertical plait set well back into aperture.

Dimensions

Holotype P302623	H 8.1	HA 5.1	W 7.0
Paratype P302624	6.9	4.4	5.4
Paratype P302627	7.2	4.5	6.5

Type material. Holotype P302623, Paratype P302624, collected T. A. Darragh, 21 February 1971; Paratype P302627, collected K. Bell & T. A. Darragh, 28 February 1970.

Type locality. PL3007.

Occurrence. PL3007 (13 specimens), PL3009 (1 specimen).

Remarks. This species closely resembles *Superstes phoenix* Finlay & Marwick, Late Eocene, New Zealand, but differs in having one prominent vertical ridge on the parietal area not two, and in having two strong central plaits flanked by two small plaits set well back in the aperture rather than three plaits as in *S. phoenix*. *S. glomerabilis* sp. nov. also has a relatively poorly developed anterior notch in the lip. Other species of *Superstes* lack parietal ridges.

The genus ranges from Early Paleocene to Late Eocene in New Zealand and hitherto has not been recorded outside New Zealand.

Family CYLICHNIDAE

Cylichnania Marwick, 1931

Type species. *Cylichnania bartrumi* Marwick, 1931, Early Miocene, New Zealand.

Cylichnania sp.

Fig. 6T–V

Description. Shell small, narrow, cylindrical. Apex with deep umbilicus. Sculpture of weak, well spaced spiral grooves over whole shell. Columella with thick narrow callus and bearing one strong fold at base. Tiny umbilical chink present, considerably encroached upon by callus.

Dimensions

Figured specimen P301973	H 10	W 4
Figured specimen P301974	11	4.5

Figured material. Figured specimen P301973, collected T. A. Darragh, 17 February 1991; Figured specimen P301974, collected T. A. Darragh, 21 November 1970.

Occurrence and material. PL3001 (2 specimens), PL3003 (9 specimens).

Remarks. All specimens either have the sculpture almost worn away or are slightly decorticated. The genus is regarded as being confined to New Zealand but there are species in the Paris Basin recorded under *Acrostemna* Cossmann or *Cylichnina* which may belong in the genus, e.g. *Bulla ambigena* Deshayes, 1862. Somewhat similar species occur in the Eocene of the southeastern United States of America recorded as *Cylichnina*, e.g. *C. galba* (Conrad, 1833). Species of *Cylichnina* are not as cylindrical as are those of *Cylichnania*.

In Australia species of the genus are known from Late Eocene through to Middle Miocene. In New Zealand the genus ranges from Paleocene to Late Miocene. The Pebble Point species is similar in shape to *C. impar* Finlay & Marwick, 1937, Paleocene, New Zealand, but the fold on the

columella seems much more prominent than on *C. impar*. It also has a much more prominent columella fold than the Australian Late Eocene *C. angustata* (Tate & Cossmann, 1897).

Priscaphander Finlay & Marwick, 1937

Type species. *Haminea cingulata* Marshall, 1917, Paleocene, New Zealand.

Priscaphander bullariformis sp. nov.

Fig. 6Q, X–Z

Description. Shell large, of average size for genus, oval, slightly tumid, involute, tapering at anterior and posterior ends, apex non-umbilicate, covered by parietal callus. Sculpture of widely spaced, narrow spiral grooves. Axial sculpture of growth lines only.

Aperture large, narrow posteriorly, very wide anteriorly; outer lip convex, apical end protruding above apex; inner lip covered with callus from apex to anterior end, callus edge sharply bounded. One short weak fold present on columella on some specimens.

Dimensions

Holotype P301975	H 17	W 10
Paratype P301976	16	9.5
Paratype P301977	20	12

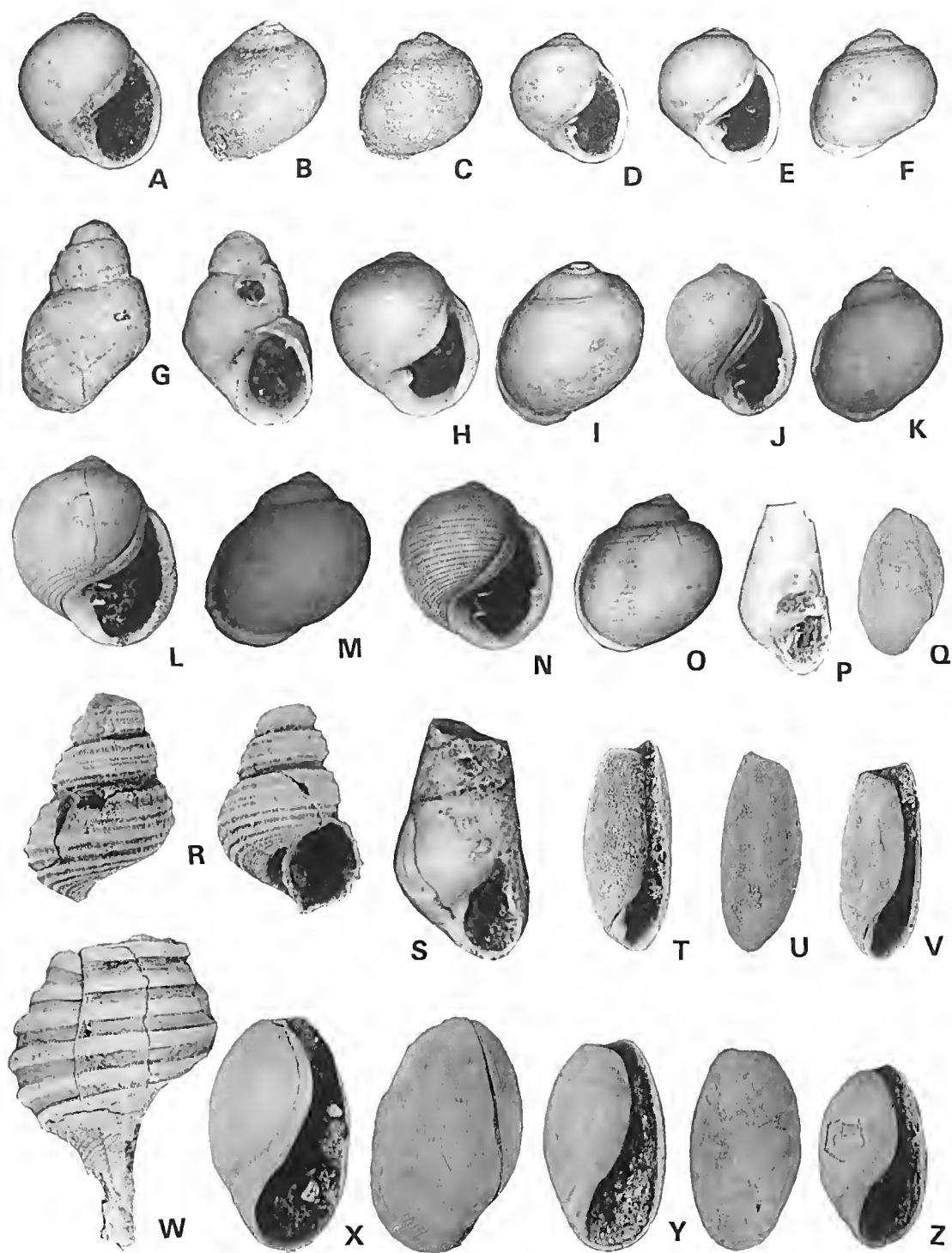
Type material. Holotype P301975, collected T. A. Darragh, 22 February 1971; Paratype P301976, collected T. A. Darragh, 13 November 1984; Paratype P301977, collected 27 November 1972.

Type locality. PL3001.

Occurrence and material. PL3001 (25 specimens), PL3003 (59 specimens), Pebble Point area unlocalised (1 specimen).

Remarks. *Priscaphander bullariformis* sp. nov. is very similar to *P. cingulata* (Marshall, 1917), but

Fig. 6. A–F, H–I, *Gilbertina meridiana* sp. nov. A–B, NMV P301972, paratype, PL3004, $\times 5.0$. C–D, NMV P301971, paratype, PL3003, $\times 4.8$. E–F, NMV P301970, paratype, PL3001, $\times 5.25$. H–I, NMV P301969, holotype, PL3003, $\times 5.0$. G, *Raulinia?* sp. NMV P301982, figured specimen, PL3003, $\times 14.3$. J–O, *Superstes glomerabilis* sp. nov. J–K, NMV P302624, paratype, PL3007, $\times 3.4$. L–M, NMV P302623, holotype, PL3007, L, $\times 3.6$, M, $\times 3.3$. N–O, NMV P302627, paratype, PL3009, N, $\times 3.5$, O, $\times 3.3$. P, S, *Odostomia* sp. P, NMV P301980, figured specimen, PL3001, $\times 8.9$. S, NMV P301979, figured specimen, PL3003, $\times 16$. Q, X–Z, *Priscaphander bullariformis* sp. nov. Q, Z NMV P301976, paratype, PL3003, Q, $\times 1.4$, Z, $\times 1.8$. X, NMV P301977, paratype, PL3003, $\times 1.8$. Y, NMV P301975, holotype, PL3001, $\times 1.8$. R, *Tuba* sp. NMV P301978, figured specimen, PL3003, $\times 2.8$. T–V, *Cylichnania* sp. T–U, NMV P301974, figured specimen, PL3001, $\times 2.9$. V, NMV P301973, figured specimen, PL3003, $\times 3$. W, gen. et sp. indet., NMV P301981, figured specimen, PL3004, $\times 1.5$.



it has much weaker spiral grooves and tapers more rapidly at the anterior and posterior ends, so that it is not so cylindrical. *P. bullariformis* is not so cylindrical and does not have such strong sculpture as *P. sanjosensis* Griffen & Hünicken from the Paleocene of Patagonia.

There seem to be no species of the genus in the Northern Hemisphere, unless the species figured as *Cylichna* sp. 1 by Kollmann and Peel (1983) from Greenland belongs. The genus has not been recorded from the Late Eocene of Antarctica. Somewhat similar shaped and sculptured species occur in the Late Cretaceous of North America which are placed in the genus *Ellipsoscapia*, Stephenson, 1941 but these have a perforate rather than an imperforate apex as in *Priscaphander*.

Family MATHILDIDAE

Tuba Lea, 1833

Type species. *T. alternata* Lea, Dec. 1833 (= *Littorina antiquata* Conrad, Sept. 1833), Eocene, United States of America.

Tuba Lea, 1833 was placed on the ICZN Official List (Opinion 436).

Tuba sp.

Fig. 6R

Description. Shell of average size for genus, conical, with strongly convex whorls. Protoconch and early spire whorls missing. Sutures impressed. Spiral sculpture of four prominent cords on spire whorls and 10 cords on last whorl, somewhat weaker and more crowded on base. Axial sculpture of thin closely spaced lamellae.

Aperture subcircular, extended anteriorly into prominent siphonal notch; siphonal fasciole broad, well developed, bounding narrow umbilicus.

Dimensions

Figured specimen P301978 H 14 est. W 6.5

Figured material. Figured specimen P301978, collected T. A. Darragh, 28 November 1972.

Occurrence and material. PL3003 (1 specimen).

Remarks. This species is similar to *Kaitangata hendersoni* Finlay & Marwick, 1937, Paleocene, New Zealand in sculpture and apertural detail but *K. hendersoni* lacks an umbilicus. *Tuba* sp. has a prominent siphonal fasciole, the whorls are much more convex, it is narrower and has two fewer cords on the spire whorls. Maxwell (1992)

synonymised *Kaitangata* Finlay & Marwick 1937, *Tuba* Lea 1833 and *Tubena* Marwick 1943 with *Gegania* Jeffreys 1884. Though preoccupied, *Tuba* was placed on the Official List and so is an available name for this group. *Tuba* has a cosmopolitan distribution in the Early Tertiary. In New Zealand *Tuba* ranges from Paleocene to Early Miocene. Stilwell & Zinsmeister (1992) have recorded both *Tubena* and *Kaitangata* from the Late Eocene of Antarctica. The Pebble Point taxon is quite unlike the Antarctic forms in having very coarse lirae. *Tuba* has not been recorded from Australia before.

Tuba sp. is very similar to *G. antiquata* Conrad 1833, Eocene, Alabama, but is more slender in outline.

There are three small fragmentary specimens which may be juveniles of this species, though the proportions do not seem to match well. These specimens have strong well spaced lirae with fine axial lamellae in the interspaces. Two have protoconchs which are deviated at 120° to the axis of the shell and are partially covered by the first teleoconch whorl.

Family PYRAMIDELLIDAE

Odostomia Fleming, 1817

Type species. *Turbo plicatus* Montagu, 1803, Recent, Europe.

Odostomia sp.

Figs 6P, S, 11D, N

Description. Shell of four to five whorls. Protoconch heterostrophic, partly immersed. Spire whorls flat with impressed suture. Last whorl flat posteriorly and contracting abruptly to base. Whorls smooth. Aperture broken. Columella with one very strong plait set well into aperture.

Dimensions

Figured specimen P301979	H 2.1	W 1.6
Figured specimen P301980	2.8	1.2
Figured specimen P302490	2.3	1.2
Figured specimen P302491	2.8	1.3

Figured material. Figured specimen P301979, collected T. A. Darragh, 24 November 1992; Figured specimen P301980, collected T. A. Darragh, 22 February 1971 (lost during photography); Figured specimens P302490–P302491, collected T. A. Darragh, 18 January 1996.

Occurrence and material. PL3001 (2 specimens), PL3003 (7 specimens), PL3004 (1 specimen).

Remarks. All specimens except three are fragments of the last whorl plus one or two other whorls. The genus has a cosmopolitan distribution. Similar looking taxa occur in the Paleocene of Mons, the Paleocene and Eocene of the Paris Basin, and the Paleocene of Greenland, Austria and West Africa. In New Zealand, the genus is known from Paleocene to Recent. In Australia species were hitherto known from Late Eocene to Recent.

Family AMATHINIDAE

Raulinia Mayer-Eymar, 1864

Type species. *Tornatella alligata* Deshayes, 1832, Oligocene, France.

Raulinia? sp.

Fig. 6G

Description. Shell thick, of small size for genus (1.4×2.1 mm), ovate. Protoconch poorly preserved, of one whorl, slightly deviated from axis of shell, slightly sunken. Teleoconch whorls 3½, sutures strongly impressed, very slightly convex.

Sculpture of widely spaced spiral punctate grooves, six on spire whorls, about 12 on last whorl.

Aperture oval; columella covered with thick callus plate; low broad plait set well into aperture. Small umbilical chink almost covered by callus.

Dimensions

Figured specimen P301982 H 2.1 W 1.4

Figured material. Figured specimen P301982, collected T. A. Darragh, 24 November 1992.

Occurrence and material. PL3003 (1 specimen).

Remarks. The single specimen is possibly a juvenile. The columella plait is set so far into the aperture that is only visible from a very oblique view of the aperture. Somewhat similar species to this occur in the Eocene and Oligocene of Europe and are placed in *Raulinia*. Other genera used for somewhat similar species are *Actaeopyramis* and *Leucotina*. It closely resembles juvenile specimens of *Raulinia eothinos* (Tate, 1894), Late Oligocene, Victoria, but these do not have the deeply impressed suture of the Pebble Point taxon.

Family SPIRATELLIDAE

Spiratella Blainville, 1817

Limacina Bosc, 1817.

Type species. *Clio helicina* Phipps, 1774, Recent, Polar seas.

Curry (1982) has shown that though Blainville's and Bosc's names were both published in December 1817, the volume containing Blainville's name was lodged in the Bibliothèque National in Paris before that containing Bosc's name. Thus *Spiratella* has priority over *Limacina*.

Spiratella advenulata sp. nov.

Fig. 7A-F

Description. Shell of average size for genus, sinistral, subglobose, somewhat planorbid, slightly wider than high; spire projecting slightly above last whorl. Whorls three to four with deeply impressed sutures. Outline of whorl more convex posteriorly. Aperture damaged, oval or reniform, produced anteriorly into lip. Umbilicus very narrow. Growth line near aperture sinuous.

Dimensions

Holotype P302009	max. W	1.6	H	0.9
Paratype P302010		1.0		0.8
Paratype P302617		1.6		
Paratype P302618		1.2		
Paratype P302619		1.5		
Paratype P302620		1.6		

Type material. Holotype P302009, collected T. A. Darragh, 24 November 1992; Paratype P302010, collected T. A. Darragh, 13 December 1994; Paratypes P302617–P302620, collected T. A. Darragh, 18 January 1996.

Occurrence and material. PL3001 (1 specimen), PL3003 (35 specimens).

Remarks. All 35 specimens are damaged. Pteropods are very rare in the Paleocene, most having been recorded from the Eocene onwards. This record may be the oldest for the genus. The only other Paleocene record of the genus is *Spiratella mercinensis* (Watelet and Lefèvre, 1885) (Curry 1965), which ranges from Latest Paleocene to Early Eocene in northwestern Europe (London Clay pteropod zone 6, latest Thanetian and Ypresian) (Janssen & King 1988). *S. advenulata* sp. nov. bears some resemblance to this taxon but is more globose, has a smaller umbilicus, narrower whorls, and the spire projects slightly. The aperture is damaged so this feature cannot be compared in detail, but it does seem to have an anterior projection somewhat similar to that in *S. mercinensis*.

S. advenulata bears some resemblance to *S. pygmaea* (Lamarck), Middle Eocene, Europe, but the spire does not project so much.

Species of *Spiratella* are recorded from Late Eocene to Middle Miocene of Australia and living in all surrounding seas. *S. advenulata* is much more globose than any of species described from the later Tertiary.

Family indeterminate

Genus and species indet.

Fig. 6W

Description. Known only from last whorl. Convex with six broad flat-topped cords, slightly narrower than interspaces. Aperture oval, produced anteriorly into short, very slightly twisted canal. Canal and base of last whorl bearing fine spiral threads much narrower than interspaces.

Dimensions

Figured specimen P301981 H31 W 21 fragment

Figured material. Figured specimen P301981, collected T. A. Darragh, 17 February 1981.

Occurrence and material. PL3001 (2 fragments of last whorl), PL3004 (1 specimen).

Remarks. The fragmentary nature of the material in hand makes comparison with other taxa almost impossible. The available material seems to bear

no resemblance to any other taxon recorded from Australia or New Zealand. What little remains of the last whorl looks a little like *Napulus fragilis* Sohl, 1964, Late Cretaceous, southeastern United States of America, but there is no trace of the axial sculpture present on species of *Napulus*.

Class Scaphopoda

Family DENTALIIDAE

Fissidentalium Fischer, 1885

Type species. *Dentalium ergasticum* Fischer, 1882, Recent, Europe.

Fissidentalium gracilicostatum Singleton, 1943

Fig. 8D-E, G-H, J-K

Fissidentalium gracilicostatum Singleton, 1943: 275, pl. 12, fig. 6a, 6b, pl. 13, fig. 9a, 9b.

Description. Shell of average size for genus (50 mm), solid, gently tapering, curved, compressed dorso-ventrally; posterior section of shell more compressed than anterior, elliptical in cross section, becoming less so anteriorly; shell wall very thick.

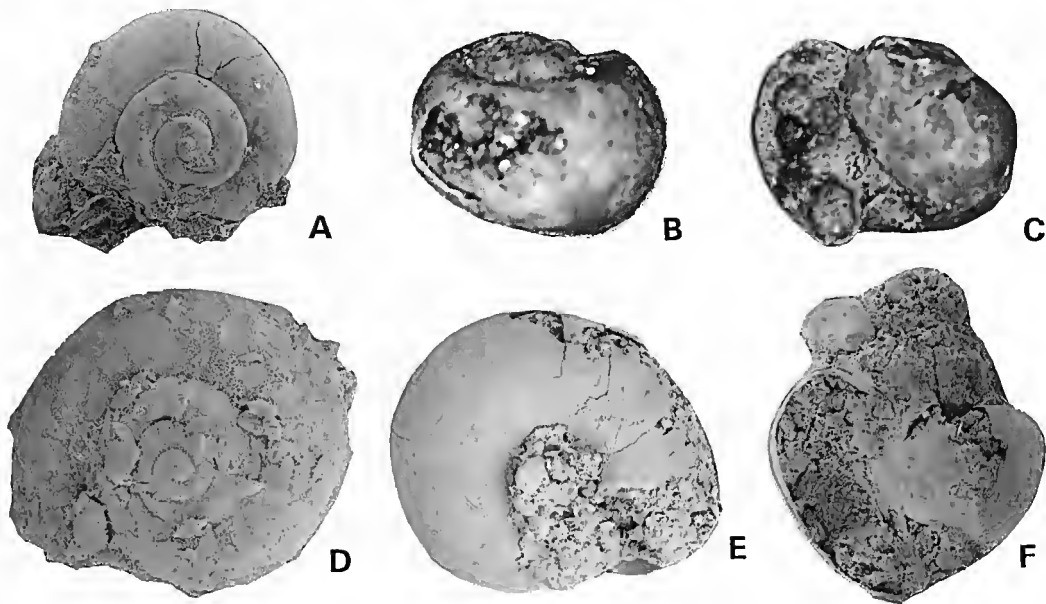


Fig. 7. A-F, *Spiratella advenulata* sp. nov., all PL3003. A, NMV P302618, paratype, $\times 30$. B-C, NMV P302009, holotype, $\times 22$. D, NMV P302619, paratype, $\times 30$. E, NMV P302617, paratype, $\times 25$. F, NMV P302620, paratype, $\times 25$.

Sculpture at extreme posterior of very fine close annular ribs, present for about 1 mm, next 0.5 mm cancellate with development of longitudinal ribs; remainder of shell with sculpture of fine close longitudinal ribs, sharply defined on posterior portion of shell, becoming wider and weaker anteriorly. On posterior part of shell two or three fine threads between strongly defined ribs, developing into wider ribs anteriorly; 30–35 primary ribs building up to 55–70 near aperture. On many specimens ribs fade out completely towards aperture.

No trace of apical slit.

Dimensions

Holotype P127989	L 21	Anterior W 5.5×5.1
		Posterior W 3.7×3.4
Figured specimen P301875	49	7.0×6.8
		2.1×1.7
Figured specimen P301876	31.7	7.6×4.5
		2.2×1.8
Figured specimen P301877	34	6.0×5.9
		1.7×1.0

Type material. Holotype P127989 (MUGD 1871), collected G. Baker, 22 January 1942; Figured specimens P301875, collected T. A. Darragh, 24 November 1992; P301876, collected T. A. Darragh & K. Bell, 28 February 1970; P301877, collected T. A. Darragh, 19 November

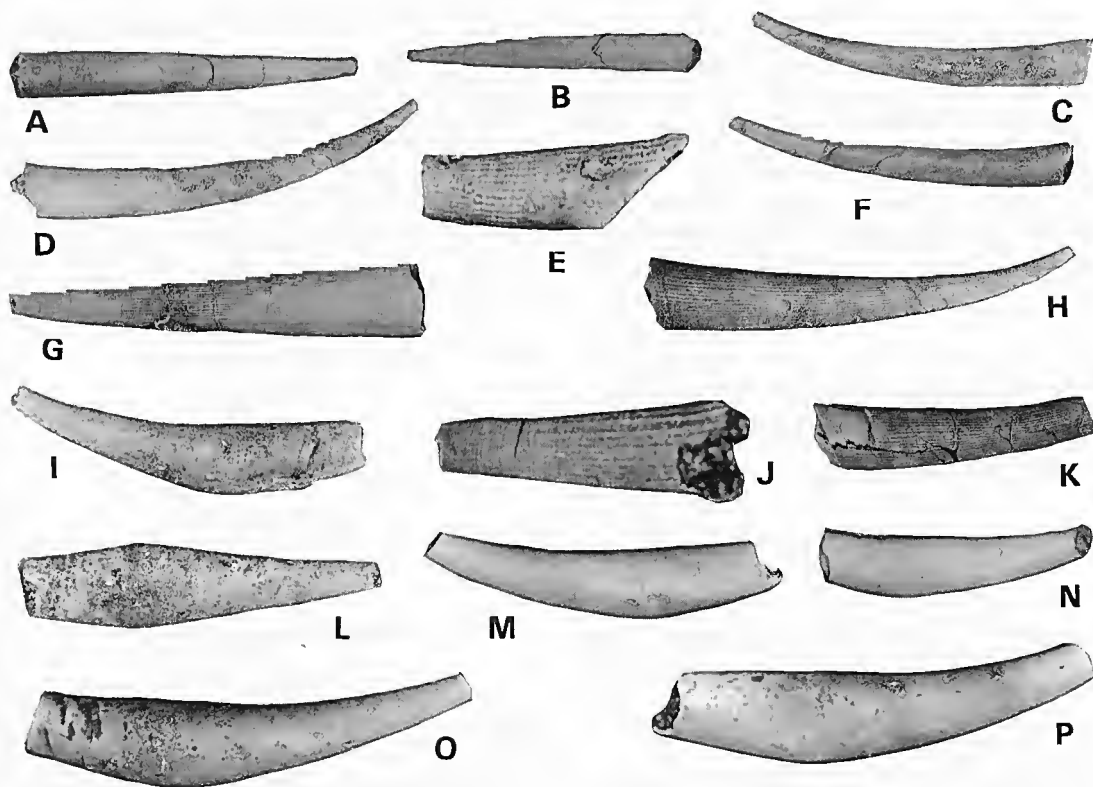


Fig. 8. A–C, F, *Compressidens laticornuta* sp. nov. A, F, NMV P301880, holotype, PL3003, $\times 1.3$. B, NMV P301879, paratype, PL3003, $\times 1.3$. C, NMV P301878, paratype, PL3003, $\times 1.3$. D–E, G–H, J–K, *Fissidentalium gracilicostatum* Singleton. D, NMV P301875, figured specimen, PL3003, $\times 1.1$. E, NMV P302631, figured specimen, apical portion showing annular ribs, PL3003, $\times 18.2$. G, NMV P301876, figured specimen, PL3001, $\times 1.7$. H, NMV P301877, figured specimen, PL3004. J, NMV P302632, figured specimen, apical portion showing annular ribs, PL3003, $\times 29$. K, NMV P127989, holotype, PL3004, $\times 1.7$. I, L–P, *Gadila laguncula* sp. nov. I, L, O, NMV P301881, holotype, I, L, $\times 6.4$, O, $\times 8.1$. M, P, NMV P301883, paratype, PL3001, M, $\times 6.6$, P, $\times 8.3$. N, NMV P301882, paratype, $\times 5.4$.

1970; P302631–P302632, collected T. A. Darragh, 13 December 1994.

Type locality. Coastal cliffs 2.5 miles south-east of Princetown, Victoria, second point north-west of Pebble Point (=PL3004).

Occurrence and material. PL3001 (10 specimens), PL3003 (39 specimens), PL3004 (15 specimens).

Remarks. *Fissidentalium gracilicostatum* seems to belong to that group of species of *Fissidentalium* that do not have an apical slit (Pilsbry & Sharp 1897; Emerson 1962). The species is more common in the formation than the above figures would suggest, because specimens are usually broken and difficult to collect. The genus is not known from the Paleocene of New Zealand nor from the late Eocene of Antarctica. Somewhat similar taxa are known from the Paleocene of southeastern USA, Copenhagen, Ukraine and the Anglo-Paris Basin, but *F. gracilicostatum* is much larger and heavier than any of these and has more ribs. *F. gracilicostatum* differs from *F. mawsoni* Ludbrook, Late Eocene to Middle Miocene, southeastern Australia, in being much more curved, in having an oval rather than circular cross section, having no fissure at the apex, and finer and more numerous ribs (50–70 as against 50). The difference between primary and secondary ribs in *F. gracilicostatum* is not very pronounced, whereas it is very pronounced in *F. mawsoni*.

Compressidens Pilsbry & Sharp, 1897

Type species. *Dentalium pressum* Pilsbry & Sharp, 1897, Recent, Caribbean.

Compressidens laticornuata sp. nov.

Fig. 8A–C, F

Description. Shell of average size for genus (25–35 mm), gently tapering, curved, compressed dorso-ventrally so as to form slight suggestion of lateral keels, lenticular in cross section; interior oval in cross section.

Sculpture of fine growth lines only. Posterior section with fine annular ribs. No slit.

Dimensions

Holotype P301880	L 34.6
	W 4.8×4.4 width at ap. 1.9×1.7
Paratype P301878	L 33
	W 5.0×4.5 width at aperture
Paratype P301879	L 29
	W 3.8×3.6 width at aperture

Type material. Holotype P301880, collected T. A. Darragh, 13 December 1994; Paratypes P301878–P301879, collected T. A. Darragh, 13 December 1984. Paratype WAM 94.403a, collected G. W. Kendrick, 13 November 1984.

Type locality. PL3003.

Occurrence and material. PL3001 (4 specimens), PL3003 (53 specimens), PL3004 (4 specimens), PL3007 (3 specimens) (Rivernook Member).

Remarks. On 12 small specimens, probably belonging to this species, the posterior section has fine rings. All other specimens are bigger than these and do not have this section preserved. Most of the specimens collected are fragments of larger specimens because they are usually cracked across the shell.

This seems to be one of three species which range from the Pebble Point Formation into the overlying Early Eocene Dilwyn Formation.

There are no taxa previously recorded from the Paleocene quite like this one. All other similar looking taxa have a circular cross section and have been placed in *Laevidentalium*. The earliest record of *Compressidens* according to Emerson (1962) is Miocene, so that the Pebble Point occurrence, if the generic assignment is correct, constitutes the earliest known. The genus is not known in the fossil record in Australia but a living species, *Compressidens platyceras* Sharp & Pilsbry, is recorded from off the coast of New South Wales. The Pebble Point taxon is about three times larger than this species and more compressed.

Family GADILIDAE

Gadila Gray, 1847

Type species. *Dentalium gadus* Montagu, 1803, Recent, Europe.

Gadila laguncula sp. nov.

Fig. 8I, L–P

Description. Shell small, of average size for genus (7 mm), solid, curved, smooth, shining, tapering towards anterior and posterior, posterior taper less than anterior, swollen at anterior $\frac{2}{3}$. Oval in cross section. Growth striae barely visible.

Dimensions

Holotype P301881	L 7.2	W 1.5
	swelling at 4.6 mm from posterior	
Paratype P301882	L 6.5	
Paratype P301883	L 7.0	W 1.5
	swelling at 5.0 mm from posterior	

Type material. Holotype P301881, collected T. A. Darragh, 13 November 1984; Paratype P301882, collected T. A. Darragh, 17 February 1981; Paratype P301883, collected T. A. Darragh & K. Bell, 21 November 1970.

Type locality. PL3001.

Occurrence and material. PL3001 (1 specimen), PL3003 (9 specimens).

Remarks. The genus has a cosmopolitan distribution (Emerson 1962). The broken specimen of *Gadila* sp. recorded from Wangaloa by Finlay & Marwick (1937) may have the swelling much closer to the anterior end than the *G. laguncula* sp. nov. *G. antarctotubula* Stilwell & Zinsmeister, late Eocene, Antarctica is more curved and more slender. *G. turgida* Meyer, Paleocene, south-eastern USA is somewhat similar in shape but *G. laguncula* is not so curved. The genus is not known from the Paleocene of the Paris Basin nor of Ukraine.

Gadila is known from the Eocene, Miocene and Pliocene of southeastern Australia. *G. laguncula* is closest to the Miocene *G. mucronata* (Tate), but the swelling is closer to the mid point of the shell than in *G. laguncula*. The Eocene species, known from one specimen, has the swelling at the mid point of the shell. There are several living species of the genus recorded from southern Australia.

Class Cephalopoda

Family NAUTILIDAE

Eutrephoceras Hyatt, 1894

Type species. *Nautilus dekayi* Morton, 1834, Late Cretaceous, United States of America.

Eutrephoceras victorianum (Teichert, 1943)

Fig. 9A–C, E, I

Nautilus victorianus Teichert, 1943: 262, pl. 11, figs 5–7. *Eutrephoceras victorianum*.—Teichert, 1947: 43, figs 5–6.

Description. Conch small for genus (maximum diameter 125), subdiscoidal, involute with small umbilicus closed by callus. Whorl outline regularly rounded ventrally, slightly flattened laterally, regularly and deeply impressed dorsally.

Siphuncle situated slightly ventral of septum centre.

Growth lines sinuous, produced aperturally on flanks, wide ventral sinus.

Sutures with low broad umbilical saddle, very broad shallow lobe laterally and shallow ventral lobe.

Dimensions

Holotype P127999	D 47	W 32
Figured specimen P301871	95	45
Figured specimen P301872	67	40

Type material. Holotype P127999, collected G. Baker, January 1942; Figured specimen P301871, collected D. J. Holloway, 14 December 1994; Figured specimen P301872, collected G. Baker, 21 February 1956.

Type locality. 'In grit band 30–40 feet above Jurassic–Tertiary unconformity. Second point north-west of Pebble Point, south-east of Princetown' (=PL3004).

Occurrence and material. PL3001 (4 specimens), PL3003 (2 specimens plus 2 fragments), PL3004 (1 specimen).

Remarks. *Eutrephoceras* ranges in age from Jurassic to Middle Miocene and has a cosmopolitan distribution. *E. victorianum* is rather laterally compressed when compared with the subglobular shape of most of the species in the genus. In shape it most resembles *E. bryani* (Gabb, 1877), Early Eocene, United States of America and *E. allani* Fleming, 1945, Early Eocene, Chatham Islands. On the basis of the two specimens of *E. allani* figured (Fleming, 1945; Stilwell & Grebneff, 1996), it seems to be very similar to *E. victorianum*.

Eutrephoceras is also known from the Early to Middle Miocene of Victoria and South Australia. *E. victorianum* is narrower and higher than *E. geelongensis* (Foord) and *E. altifrons* (Chapman) and has slightly more sinuous sutures than these Neogene species.

Aturoidea Vredenburg, 1925

Type species. *Nautilus parkinsoni* Edwards, 1849, Eocene, England.

Aturoidea distans Teichert, 1943

Figs 9D, F–H, 10A–C

Aturoidea distans Teichert, 1943: 260, pl. 11, figs 1–4, fig. 1.—Teichert 1947: 40, figs 1–4.

Description. Conch very large (300+ mm diameter), subdiscoidal, moderately broad, involute, umbilicus closed.

Whorl outline regularly rounded ventrally, somewhat flattened laterally, sides diverging then rapidly contracting to umbilicus.

Suture with broad almost flat ventral saddle; lateral lobe narrow, elongate, asymmetrically attenuating; lateral saddle broad, strongly and regularly curved; umbilical lobe narrow, strongly curved; umbilical saddle narrow, strongly curved; dorsal lobe deep, narrow with parallel sides.

Siphuncle with orthochoanitic septal necks, situated close to dorsum; septal necks curved, long, one third to half length of camerae; connecting rings cylindrical, considerably overlapping septal necks and invaginating into preceding septal foramina.

Growth lines sinuous, strongly convex laterally then swinging backward to form deep hyponomic sinus.

Dimensions

Holotype P123012	D 110	W 50 (as preserved)
Figured specimen P301860	127	73
Figured specimen P128060	299	146

Type material. Holotype P123012 (formerly MUGD 1860), Paratype 123013 (MUGD 1861), Paratype P123014 (MUGD 1862), all collected G. Baker, January 1942; Figured specimen P128061 (MUGD 1932) (Teichert 1947, figs 3–4), collected O. P. Singleton, 1943; P128060 (MUGD 1931) (Teichert 1947, figs 1–2); Figured specimen P301860, collected T. A. Darragh, 2 December 1985; P301865, collected T. A. Darragh, 8 March 1977.

Type locality. 'Grit band, 30–40 feet above unconformity between Jurassic (i.e. Lower Cretaceous) and Tertiary. Second point north-west of Pebble Point, south-east of Princetown, Victoria', i.e. PL3004.

Occurrence and material. PL3001 (1 specimen), PL3003 (5 specimens), PL3004 (1 specimen), Pebble Point area (8 specimens), Killara Bluff (1 specimen).

Remarks. *Aturoidea* ranges in age from Late Cretaceous to Middle Eocene, but most species seem to have been recorded from rocks now known to be of Paleocene age. The genus has a cosmopolitan distribution having been found in England, Spain, Bulgaria, Libya, Angola, Pakistan, India, New Zealand, California, New Jersey and Australia. However, most species are represented by only one or two specimens, except in Western Australia and Victoria where species are represented by up to a 16 specimens.

Teichert's original illustration of the suture of *A. distans* is not correct. The lateral lobes

are not narrow and pointed, but asymmetrically attenuated just as in the type species *Aturoidea parkinsoni* (Edwards). According to Miller (1947), *A. parkinsoni*, *A. spathi*, *A. pilsbryi* and *A. paucifax* are all similar and not very different in age. *A. distans* can also be added to this list, as well as *A. brunnschweileri* Glenister, Miller & Furnish, from the Middle Eocene of Western Australia. Glenister et al. (1956) distinguished their species from *A. distans* by the differences in the shape of the suture of *A. distans* as described by Teichert. In fact the sutures of both species are very similar if not identical.

A small specimen of what seems to be this species occurs in the Early Eocene Rivernook Member of the Dilwyn Formation which overlies the Pebble Point Formation.

Aturoidea is not found above the Early Eocene in Eastern Australia.

Bivalvia

Family NUCULIDAE

Nucula Lamarck 1799

Type species. *Arca nucleus* Linnaeus, 1758, Recent, Europe.

Nucula sp.

Fig. 12B-C

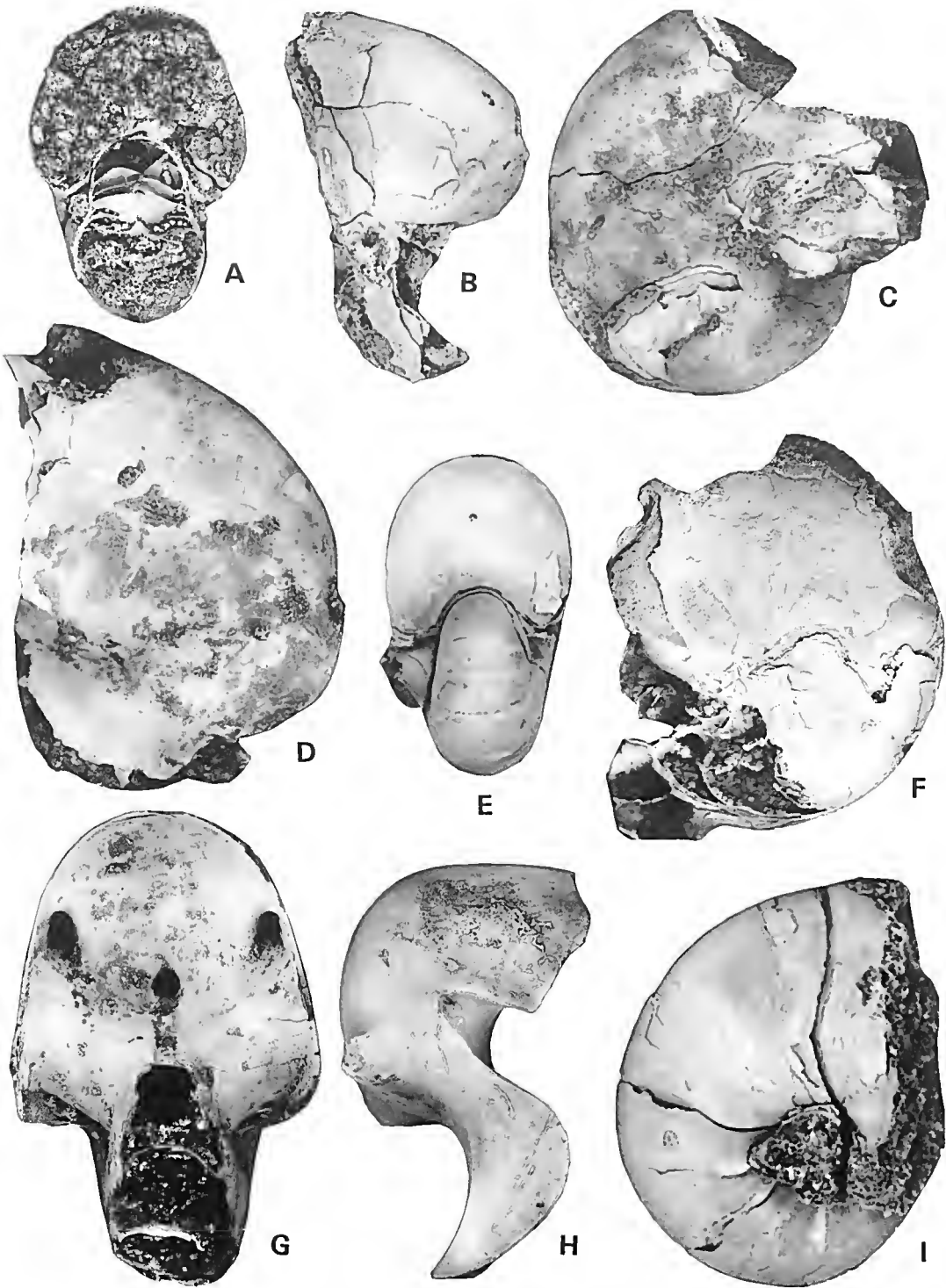
Dimensions

Figured specimen P302630	W 2.1	H 2.2
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Figured material. Figured specimen P302630, collected T. A. Darragh, 24 November 1992.

Remarks. The collection of additional material has permitted the confirmation of a second nuculid in the fauna. There are six specimens in hand, most of which are broken, ranging in size from 3×2.4 mm to an estimated 6×5.5 mm. This species belongs in *Nucula* s.s. The surface of the valve is almost smooth and covered with numerous closely spaced, very faint radial lines. Some specimens have coarse growth lines. The internal margin of the valve is denticulate. It bears considerable resemblance to European species of

Fig. 9. A–C, E, I, *Eutrophoceras victorianum* Teichert. A–B, NMV P127999, holotype, PL3004, A, ×1.0, B, ×1.4. C, NMV P301871, figured specimen, PL3001, ×0.6. E, I, NMV P301872, figured specimen, PL3003, E (first chamber removed), ×0.7, I (first chamber in place), ×0.9. D, F–H, *Aturoidea distans* Teichert. D, G, NMV P301860, figured specimen, PL3003, D, ×0.6, G, ×0.6. F, NMV P123012, holotype, PL3004, ×0.7. H, NMV P301865, figured specimen, PL3003, ×0.5.



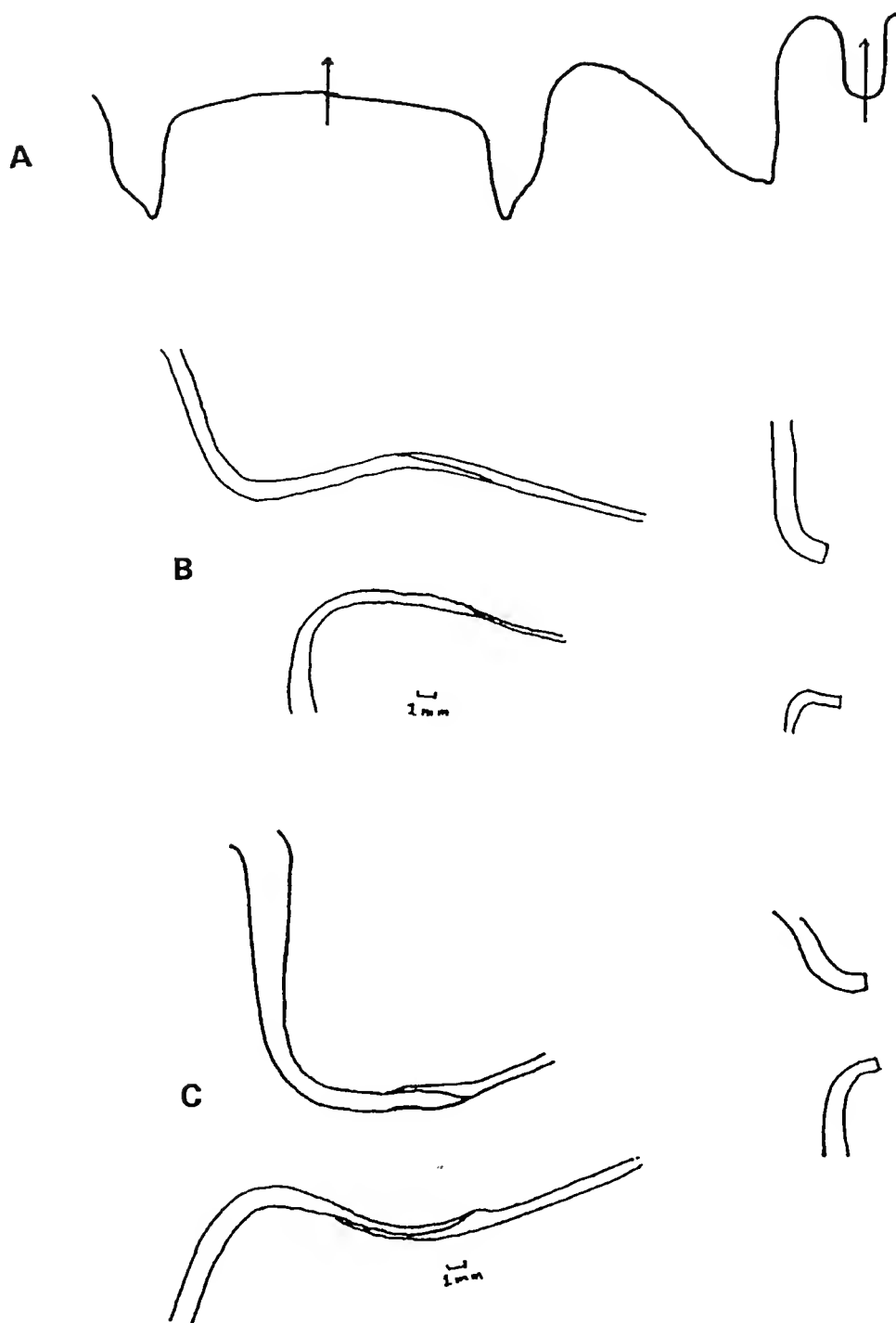


Fig. 10. A-C, *Aturoidea distans* Teichert. A, sketch of suture based on P301864. B-C, sketch of both sides of longitudinal section cut through siphuncle of P301863 showing attachment of septal ring to septal neck.

Nucula from the Paleocene and Eocene, such as *N. montensis* Cossmann (Paleocene, Belgium) and *N. fragilis* Deshayes (Paleocene-Eocene, Europe). This species is bigger and more triangular than *Lamellinucula pyrenoides* Darragh, Pebble Point Formation, and lacks the sharp, raised commarginal ribs.

Two specimens have gastropod boreholes.

Austronucula Powell, 1939

Type species. Austronucula schenki Powell, 1939, Recent, New Zealand.

Austronucula? arenaria sp. nov.

Fig. 11G-I

Description. Shell minute (0.9×0.8–1.3×1.1 mm), very solid, porcellanous, trigonal. Umbones orthogyral. Anterior dorsal margin straight; anterior margin short, rounded, merging imperceptibly with dorsal and ventral margins; posterior dorsal margin straight, longer than anterior dorsal margin; posterior margin short, rounded, merging imperceptibly with dorsal and ventral margins; ventral margin gently curved. Hinge separated into two parts by deep triangular vertical ligament pit; pit apex directed dorsally and pit sunk well below hingeline. Anterior tooth row with five to six teeth, posterior row with three teeth. Muscle impressions subequal, slightly oval; posterior adductor impression very deep. Pallial line entire. Inner ventral margin smooth. Internal surface of valve shining. External surface of valves shining, smooth, except for traces of fine growth striae.

Dimensions

Holotype P302282	W 0.9	H 0.9 pair
Paratype P302283	0.9	0.9
Paratype P302284	0.8	0.8

Type material. Holotype P302282, Paratype P302283, Paratype P302284, collected T. A. Darragh, 13 December 1994.

Type locality. PL3003.

Occurrence and material. PL3003 (77 specimens).

Remarks. The combination of small size and absence of any radial elements in the shell structure, absence of marginal denticulations and external sculpture in *Austronucula? arenaria* sp. nov. is quite unlike the characters of any other Australian nuculid so far recorded. The species is placed in *Austronucula* with some hesitation. Previously *Austronucula* has been recorded only from New Zealand. *A.? arenaria*

is more triangular than either of the two New Zealand species and lacks the prominent prodissoconch of these species. It has more teeth than *A. schencki* Powell, in which respect it resembles *A. galathea* Dell.

The material can be grouped into two. One group consists of very well preserved smooth shining valves, amongst which articulated valves are not uncommon. The second group consists of larger valves which are invariably worn, pitted and coloured green. Glauconite is deposited in pits and sockets and attached to the internal and external surfaces of the valves in the second group. The calcite in some specimens of this group may have been replaced by glauconite.

Family NUCULANIDAE

Comitileda Iredale, 1924

Type species. Leda miliacea Hedley, 1902, Recent, New South Wales.

Until a proper revision of the small rostrate nuculanids is undertaken, I follow Maxwell (1992) in using this genus rather than *Ledina* to which Australian species have been previously assigned. The genus occurs in New Zealand from Middle Eocene to Recent and in Australia from Paleocene to Recent.

Comitileda brachyrhynchoides sp. nov.

Fig. 11K-L

Comitileda sp. cf. *C. brachyryncha* Maxwell, 1992.—Darragh, 1994: p. 77, fig. 1K-M.

Description. Shell small (2–3 mm), ovate, almost equilateral, somewhat tumid, slightly rostrate at posterior end. Umbo central, projecting slightly, very slightly opisthogyral. Anterior dorsal margin gently convex; anterior margin strongly convex, merging into convex ventral margin; ventral margin gently convex, concave where it merges with posterior margin; posterior dorsal margin straight; posterior margin short, strongly convex. Surface of valve smooth except for growth ridges. Hinge with ten posterior and eight anterior chevron-shaped teeth, apex directed towards umbo. Muscle scars subequal, barely visible; pallial line with shallow rounded sinus. Internal valve margin smooth.

Dimensions

Holotype P302325	L 3.3	H 2.1
Paratype P302326	2.75	1.7
Paratype P142862	2.2	1.4 pair

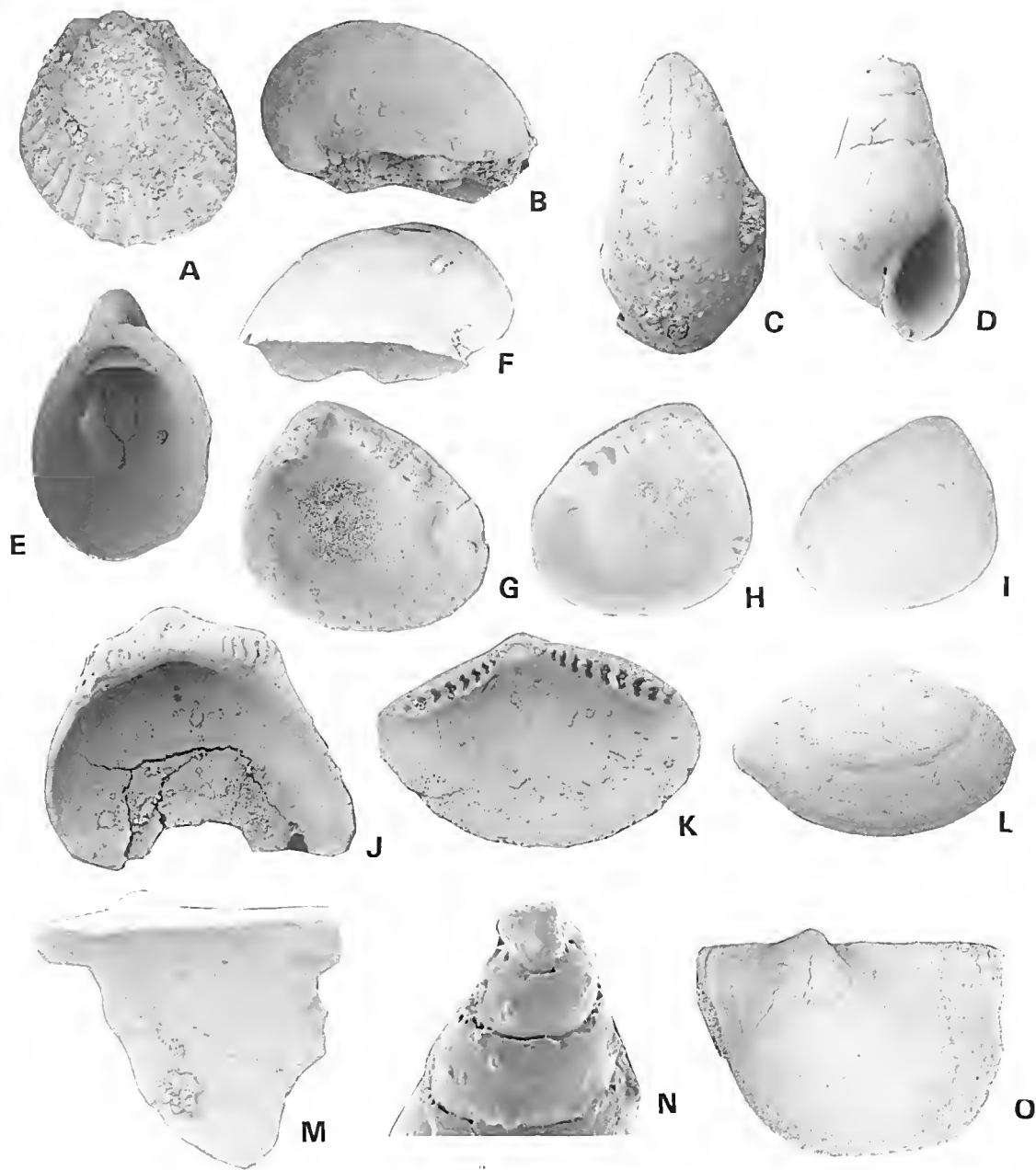


Fig. 11. A, J, *Limea (Notolimea) multicostulifera* sp. nov. A, NMV P302277, holotype, PL3003, $\times 17$. J, NMV P302278, paratype, PL3003, $\times 25$. B-C, E-F, *Rimula? crepiduloides* sp. nov. B, P302612, paratype, PL3003, $\times 20$. C, NMV P302613, holotype, PL3003, $\times 17$. E-F, specimen lost in scanning, PL3003, $\times 30$. D, N, *Odostomia* sp. D, P302490, figured specimen, PL3003, $\times 17$. N, NMV P302491, figured specimen, PL3003, $\times 47$. G-I, *Austronucula? arenaria* sp. nov. G, NMV P302283, paratype, PL3003, $\times 39$. H, NMV P302284, paratype, PL3003, $\times 39$. I, P302282, holotype, PL3003, $\times 35$. K-L, *Comitileda brachyrhynchoides* sp. nov. K, NMV P302326, paratype, PL3003, $\times 17$. L, NMV P302325, holotype, PL3003, $\times 12.5$. M, O, *Electroma glessaria* sp. nov. M, P302281, paratype, PL3003, $\times 15$. O, NMV P302280, holotype, PL3003, $\times 25$.

Type material. Holotype P302325, Paratype P302326, collected T. A. Darragh, 18 January 1996; Paratype P142862, collected T. A. Darragh, 24 November 1992.

Occurrence and material. PL3003 (26 specimens).

Remarks. Three specimens have countersunk gastropod drill holes. *Comitileda brachyrhynchoidea* sp. nov. bears a very close resemblance to *C. brachyryncha* Maxwell, Eocene, New Zealand but differs by being slightly more elongate and having a more convex anterior margin. It is also very similar to *C. praelonga* Tate, Oligocene to Miocene, Australia. *C. praelonga* is more rostrate, more slender and more pointed at the posterior end, but the differences are slight. *C. brachyrhynchoidea* is more tumid than *C. miliacea* (Hedley) but is not as elongate and the umbo is not so strongly opisthogyal. *Leda rhamphidia* Cossmann, Paleocene, Belgium is somewhat similar in shape to *C. miliacea*.

Family GLYCYMERIDAE

Glycymeris Da Costa 1778

Type species. *Arca glycymeris* Linnaeus, 1758, Recent, Europe.

Glycymeris sp.

Fig. 12I, P

Description. Shell of medium size for genus (48×51 mm), rounded, slightly higher than wide, umbo projecting. Sculpture, poorly preserved, seemingly of wide, low costae, separated by very narrow shallow grooves. Hinge arched, bearing about five teeth in each series.

Dimensions

Figured specimen P302275 W 48 H 51 T 23 approx.

Figured material. Figured specimen P302275, collected T. A. Darragh, 14 December 1994.

Occurrence and material. PL3001 (1 specimen and 1 fragment).

Remarks. The material in hand is poorly preserved and somewhat weathered. One specimen is a complete valve and the other specimen is a valve fragment. This species is about the same size as *Glycymeris concava* Marshall, 1917, Early Paleocene, New Zealand, type species of *Glycymerita* Finlay & Marwick, 1937, but it has a rounded rather than quadrate outline and the radial sculpture does not seem to be so well developed and so is not related.

Of Australian Tertiary taxa, it has some resemblance to *G. cainozoica* Tenison Woods, 1877, from the Late Oligocene to Middle Miocene of Victoria and Tasmania, but is more robust than that species.

Glycymeris has a cosmopolitan distribution from Late Cretaceous on. Somewhat similar looking species, but not so robust are known from the Paleocene of Belgium, Denmark and Ukraine. It is very similar to *G. erebratularis* (Lamarck, 1829) from the Thanetian of the Paris Basin.

Family PTERIIDAE

Electroma Stoliczka, 1871

Type species. *Avicula smaragdina* Reeve, 1857, Recent, Indonesia.

Pterelectroma Iredale 1939: 332.

Electroma glessaria sp. nov.

Fig. 11M, O

Electroma sp. Darragh, 1994: 84, fig. 3C–D, 1.

Description. Shell small, thin, naereous, oblique, inequivalve; left valve inflated, right valve relatively flat; anterior of valves with triangular wing separated from flank of valve by slight sinus. Umbo projecting slightly above hinge line, opisthogyal. Hinge long and straight with triangular posteriorly directed resilifer pit under umbo, slightly anterior of mid point of hinge. Hinge with long posterior lateral and one very short anterior lateral in left valve. Posterior adductor muscle impression large; anterior adductor impression very small, situated high under hinge, slightly anterior of umbo; other internal features of valve not preserved. Byssal notch very shallow. External surface of valve smooth.

Dimensions

	L	W
Holotype P302280	1.8	1.4
Paratype P302281	3.0	3.1 broken
Paratype P142966	1.4	1.2
Paratype P142965	4.5+	2.5+

Type material. Holotype P302280, Paratype P302281, collected T. A. Darragh, 18 January 1996; Paratypes P142965–P142966, collected T. A. Darragh, 24 November 1992.

Type locality. PL3003.

Occurrence and material. PL3003 (32 valves and one pair).

Remarks. All specimens are small and are almost certainly juveniles. Only two valves are sufficiently complete and large enough for comparison with other taxa. *Electroma glessaria* sp. nov. seems similar to Palaeogene species assigned to *Electroma* Stoliczka, though *Pteria* Scopoli, 1777 has also been used for such species and may well be the correct taxon. The anterior of the valve is slightly more produced than in

juveniles of *Electroma georgiana* (Quoy & Gaimard), living, southern Australia, and the central part of the valve is much more convex (higher). In this respect it is somewhat similar to *E. zebra* (Reeve), Recent, Queensland.

In shape *E. glessaria* is similar to *E. stam-pinensis* (Deshayes), Early Oligocene, Europe, but it is not so oblique as other Eocene taxa assigned to *Electroma* by Glibert and Van der Poel (1965).

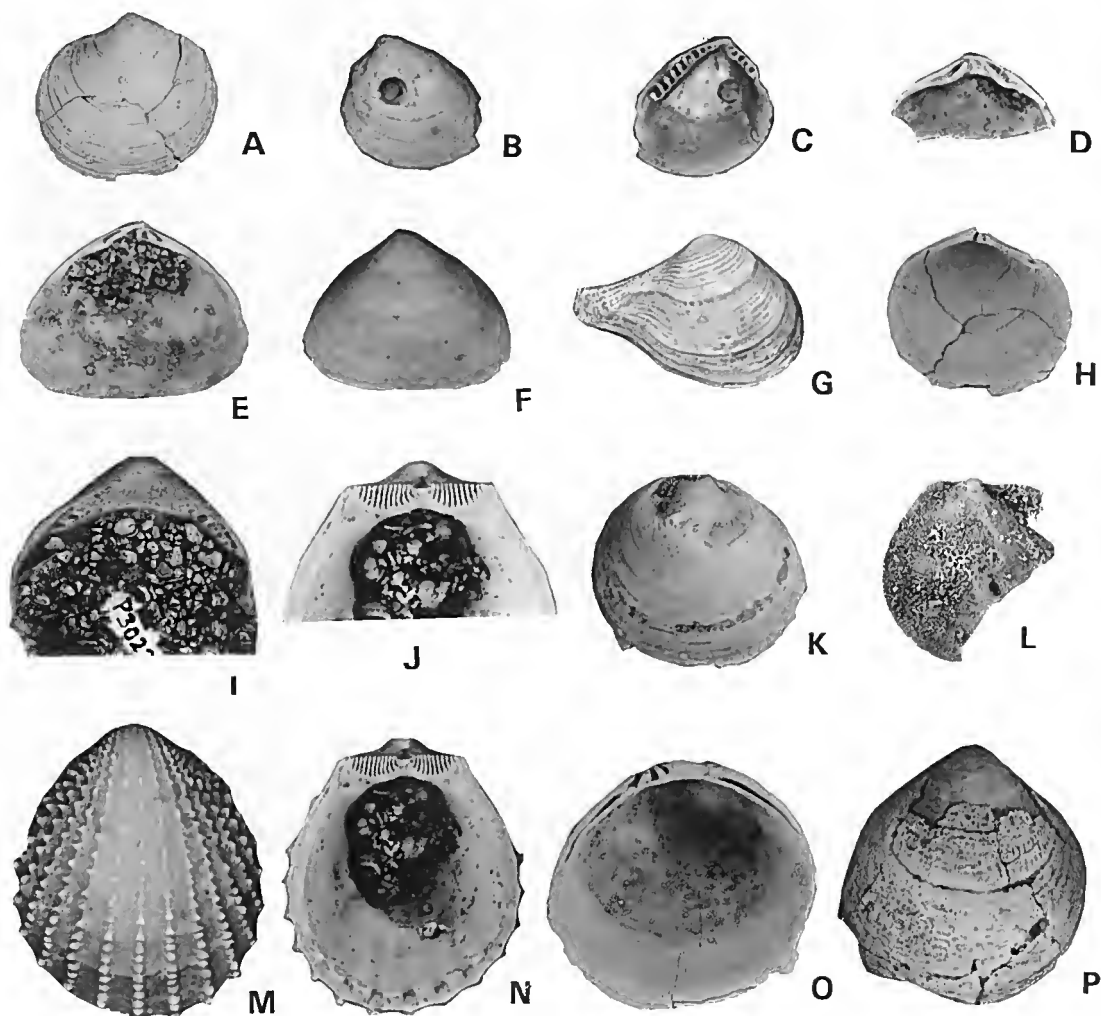


Fig. 12. A, H, *Jagolucina psephenata* sp. nov. NMV P301795, holotype, PL3003, $\times 3.1$. B-C, *Nucula* sp., NMV P302630, figured specimen, PL3003, $\times 5.1$. D-F, *Bornia flabellaris* sp. nov. D, NMV P302271, paratype, PL3003, $\times 8.4$. E-F, NMV P302270, holotype, PL3003, E, $\times 8.2$, F, $\times 7.5$. G, *Cuspidaria obbata* sp. nov. NMV P301644, holotype, PL3003, $\times 2.5$. I, P, *Glycymeris* sp. NMV P302275, figured specimen, PL3001, $\times 0.7$. J, M-N, *Limea (Notolimea) australis* (Smith), Australian Museum C26640, 1463 m, 35 miles east of Sydney, NSW, $33^{\circ}51'S, 151^{\circ}58'-152^{\circ}0'E$. K, O, *Corbicula?* sp. NMV P302276, figured specimen, PL3003, K, $\times 2.3$, O, $\times 2.8$. L, *Delectopecten* sp. NMV P302628, figured specimen, PL3003, $\times 5.1$.

It has a smaller anterior wing and is more rectangular in shape than *E. intacta* Finlay and Marwick, Wangaloan, New Zealand. *E. notiala* Stilwell and Zinsmeister, Late Eocene, Seymour Island, is much more oblique than the Pebble Point taxon. Despite the ambiguity in generic determination, i.e. whether *Pteria* or *Electroma*, it is clear that the Pebble Point taxon belongs to a group that was widespread in the early Palaeogene.

Family PECTINIDAE

Delectopecten Stewart, 1930

Type species. *Pecten (Pseudamussium) vancouverensis* Whiteaves, 1893, Recent, North eastern Pacific.

Delectopecten sp.

Fig. 12L

Description. Shell of average size for genus, thin, fragile, equivalve except for byssal notch, ovate, slightly produced posteriorly. Posterior car of both valves small, not well defined. Sculpture of 'camptonectes' striae only.

Dimensions

Figured specimen P302628 L 4.5 est. H 4.6

Figured material. Figured specimen P302628, collected T. A. Darragh, 18 January 1996.

Material. PL3003 (4 specimens and fragments).

Remarks. *Delectopecten* has a very wide distribution. It is known living from the Indian Ocean, the north and eastern Pacific Ocean and from northern Australia, New Caledonia and New Zealand. It occurs from Eocene to Holocene in Western North America, in the Miocene of Europe and in the Oligocene and Miocene of Japan and eastern Russia.

This species will be described in more detail and illustrated with better material in a publication with A. G. Beu on Australian Tertiary Pectinidae.

Family LIMIDAE

Limea (Notolimea) Iredale, 1924

Type species. *Lima australis* Smith, 1891, Recent, New South Wales.

Limea (Notolimea) multicostulifera sp. nov.

Fig. 11A, J

Limid indet. Darragh, 1994: 85, fig. 3E.

Description. Shell small (2.2×2.6–2.9×3.6 mm), very slightly inequilateral, oval, slightly higher than wide; umbo somewhat inflated, orthogyral, projecting very slightly above hinge margin; auricles small, subequal. Approximately 24 to 30 radial ribs, thin and crowded on anterior and posterior flanks, broad and widely spaced on central flank. Ligamental area, centrally situated, triangular; eight to nine vertical teeth on each side of hinge, no teeth below ligament pit. Internal features of valves crocod. Internal valve margin denticulate.

Dimensions

Holotype P302277	L 2.9	H 3.6
Paratype P142881	2.4 est.	2.3+

Type material. Holotype P302277, Paratype P302278, collected T. A. Darragh, 18 January 1996; Paratype P142881, collected T. A. Darragh, 24 November 1992.

Occurrence and material. PL3001 (1 specimen); PL3003 (71 specimens); PL3004 (1 specimen).

Remarks. Most specimens are worn or decorticated and fragmentary, and consist of the umbonal or dorsal half of the valve suggesting that they may have travelled some distance before burial. One specimen shows traces of tubercles on the ribs. *Limea (Notolimea) multicostulifera* sp. nov. closely resembles the type species of *Notolimea*, *Limea australis*, but *L. (N.) multicostulifera* has 24 to 30 ribs compared with 17 to 18 in *N. australis* and it lacks the tubercles of that species except on one specimen. The hinge is identical to that of *N. australis*. The shell structure of *N. australis* consists of two parts; an internal white opaque layer and an external translucent layer. The fossil material seems to consist mostly of the internal opaque layer, the outer layer having been lost.

Species of *Notolimea* are known from the Eocene to Miocene of Europe. Of these *L. (N.) sacki* (Philippi), Early Oligocene, Germany, is similar in size and hinge morphology, but *L. (N.) multicostulifera* has thinner ribs, no secondary intercalated ribs and the ribs are not tuberculate as in *N. (L.) sacki*. Two other similar species, *N. (L.) eocenica* (de Laubrière) and *N. (L.) tenuisculptata* (Cossmann), occur in the Middle Eocene of the Paris Basin. *N. broccha* Marwick, 1931 occurs in the Middle Miocene of New Zealand.

In the Tertiary of southeastern Australia, there is only one species of *Notolimea* recorded so far. This is *Limea (Notolimea) alticosta* Tate which is similar in overall morphology to *L. (N.) multicostulifera* but has fewer ribs (14).

As the type species of this subgenus has never been adequately figured, figures of the exterior and interior are provided from a specimen dredged from 1463 m, 35 miles east of Sydney, NSW (Fig. 12J, M–N).

Family LUCINIDAE

Jagolucina Chavan, 1939

Type species. *Lucina concava* DeFrance, 1823, Eocene, France.

Jagolucina? *psephenata* sp. nov.

Fig. 12A, H

Jagolucina? sp. Darragh, 1994: 87, fig. 4E, G.

Description. Shell subcircular, of average size (6–10 mm), moderately inflated; umbo pointed, prosogyral; anterior dorsal margin concave; anterior, ventral and posterior margins regularly convex, not differentiated from one another; posterior dorsal margin straight. Lunule short, prominent. Sculpture of fine, close set, com-marginal ribs.

Hinge: left valve with bifid anterior cardinal; thin posterior cardinal; two anterior laterals separated by short socket; possibly one posterior lateral.

Anterior muscle scar long, narrow, divergent from pallial line, extending from under anterior lateral tooth well into valve. Posterior scar lozenge-shaped, not clearly visible.

Internal margin of shell smooth.

Dimension

Holotype P301795	L 7.5	H 7.2
Paratype P142890	6.5	6
Measured specimen P142891	11.2	10.5

Type material. Holotype collected W. J. Parr, 11 January 1943; Paratype P142890, collected T. A. Darragh, 13 November 1984.

Type locality. Fourth point south-east of the mouth of the Gellibrand River (i.e. PL3003).

Occurrence and material. PL3001 (two left valves), PL3003 (10 left and three right valves).

Remarks. Additional material of this species found in the collections has permitted it to be

formally described. All specimens except the holotype are very worn and the generic position is very much open to doubt. Three of the left valves have gastropod boreholes. I have found no obviously related species in the Southern Hemisphere. *Jagolucina* occurs in the Paleocene and Eocene of Europe.

Family ERYCINIDAE

Bornia Philippi, 1836

Type species. *Bornia corbuloides* Philippi, 1836 (= *Cyclas sebetia* Costa, 1829), Recent.

Bornia flabellaris sp. nov.

Fig. 12D–F

Borniola? Darragh, 1994: 89, fig. 4N–O.

Description. Shell triangular, of average size for the genus; umbo pointed, slightly projecting, slightly prosogyral; valve strongly convex at flanks, central part of the disk flattened or slightly depressed; posterior dorsal margin straight, posterior and anterior margins short, strongly convex; ventral margin slightly concave.

Hinge: left valve with prominent long posterior tooth; central triangular resilifer flanked anteriorly by short curved tooth, separated by narrow socket from strong anterior tooth. Right valve with deep anterior socket, flanked posteriorly by strong, short, projecting, curved tooth; wide central triangular resilifer, flanked posteriorly by long strong lateral, lateral flanked posteriorly by long deep socket. Muscle scars subequal, situated high in valve. Pallial line entire. Sculpture of growth lines only.

Dimensions

Holotype P302270	L 3.6	H 2.8
Paratype P302271	3	3 fragment only
Paratype P142899	4.1	3.5

Type material. Holotype P302270, Paratype P302271, collected T. A. Darragh, 18 January 1996; Paratype P142899, collected T. A. Darragh, 13 November 1984.

Type locality. PL3003.

Occurrence and material. PL3003 (14 specimens).

Remarks. Since the first record of this taxon, more material has been collected which enables a more precise determination to be made. The hinge is very similar to the type species of the genus, *Bornia sebetia*, the teeth being virtually identical, however the resilifer pit is very short in the type

species and long in *B. flabellaris* sp. nov. Compared with *Bornia trigonalis* (Tate), Recent, southern Australia, *B. flabellaris* is more triangular in outline and the resilifer pit is larger. It also lacks the fine reticulate sculpture of *B. trigonalis*.

The genus is known from Eocene to Recent in Europe and United States of America and has a cosmopolitan distribution in Recent seas. There are probable unrecorded species of the genus in the Tertiary of southeastern Australia.

Family CORBICULIDAE

Corbicula Mergele von Mühlfeld, 1811

Type species. Tellina fluminalis Müllcr, 1774, Recent, Middle East.

Corbicula ? sp.

Fig. 12K, O

Description. Shell subcircular, somewhat globose, of small size for genus (11×12 mm). Umbonal region corroded. Sculpture of growth lines only.

Hinge: right valve with long anterior deep cross-grooved socket, very weak thin anterior cardinal, separated by wide socket from strong bifid cardinal; posterior cardinal weakly bifid separated from central cardinal by wide socket and flanked on posterior by narrow triangular socket; posterior socket long and cross-grooved.

RV 0 0 / \ 010 →

Internal margin of valve smooth. Muscle scars subequal; anterior slightly longer than width; posterior scar D-shaped, slightly larger than anterior scar. Pallial line possibly with a shallow sinus.

Dimensions

Figured specimen P302276 W 12 H 11 T 3

Figured material. Figured specimen P302276, collected T. A. Darragh, 18 January 1996.

Material and occurrence. PL3003 (1 specimen).

Remarks. This has some resemblance to small specimens of *Corbicula gravesi* (Deshayes, 1825), Early Eocene, Paris Basin, but is not so globose, has a rounded outline and the cardinal teeth are directed vertically not anteriorly as in *C. gravesi*.

Corbicula is known from the Paleocene and Eocene of Europe and the Paleocene and Eocene of the United States of America. Modern species

of the genus are found in brackish and fresh water, whereas Early Tertiary species are found in marine sediments as well as in sediments of fresh and brackish water origin. The single specimen from the Pebble Point Formation has a corroded umbonal region which suggests that it may have originated in a fresh or brackish water environment and been washed into the sea.

Family CUSPIDARIIDAE

Cuspidaria Nardo, 1840

Type species. Tellina cuspidata Oliv., 1792, Recent, Mediterranean.

Cuspidaria obbata sp. nov.

Fig. 12G

Cuspidaria sp. Darragh, 1994: 101, fig. 8A–C, E–F.

Description. Shell elongate ovate, rostrate, tumid, of average size for genus (11×7.7 mm); umbo opisthogyral, not projecting; anterior dorsal margin long convex; anterior margin short, strongly convex, continuous with dorsal margin; ventral margin convex then concave where it forms posterior rostrum; posterior dorsal margin concave extending to form posterior rostrum. Sculpture of thin, widely spaced, commarginal ribs present either on dorsal third of valve only or over whole of valve, other portion of valve sculptured with prominent growth ridges. Rostrum with three to five fine widely spaced radial threads, one of which bounds rostrum ventrally. Hinge with small resilifer under umbo, teeth if present in left valve not visible on available material. Right valve with long posterior lateral tooth. Posterior adductor scar subtriangular deeply sunken; anterior scar not visible.

Dimensions

Holotype P301644	L 11.7	H 7.7
Paratype P142946	10	6.5
Paratype P142948	9.5	7
Paratype P142951	8	5.5

Type material. Holotype P301644, collected T. A. Darragh, 13 December 1994; Paratypes P142946, P142948, P142950, collected T. A. Darragh, 23 November 1992.

Type locality. PL3003.

Occurrence and material. PL3001 (1 specimen), PL3003 (5 specimens), PL3004 (1 specimen).

Remarks. Additional material enables this species to be formally described. Three specimens are

left valves and are incomplete or worn. Two right valve are complete and unworn. This taxon is very close in morphology to *Cuspidaria subrostrata* Tate, Middle Miocene, Victoria. The sculpture is similar but the outline is subcircular rather than elliptical. In shape it resembles *Cuspidaria raincourtii* Cossmann, Eocene, Paris Basin, but that species has close-set, fine commarginal ribs covering the whole valve. The genus occurs rarely in the Paleocene of Europe and has been recorded from the Paleocene of Pitt Island, New Zealand (Campbell et al. 1993), but it is not recorded from the Early Tertiary of mainland New Zealand, Antarctica or from the Paleocene of the United States.

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MYRIOTROCHUS ANTARCTICUS SP. NOV. (APODIDA: MYRIOTROCHIDAE),
A NEW HOLOTHURIAN SPECIES FROM EASTERN ANTARCTICA

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SMIRNOV, A. & BARDSLEY, T. M., 1997:11:30. *Myriotrochus antarcticus* sp. nov. (Apodida: Myriotrochidae), a new holothurian species from eastern Antarctica. *Proceedings of the Royal Society of Victoria*. 109 (1): 109–111. ISSN 0035-9211.

Myriotrochus antarcticus sp. nov. from eastern Antarctica is described. *Myriotrochus antarcticus* is the first myriotrochid species to be recorded from the continental shelf in the Southern Hemisphere.

ANTARCTIC benthic invertebrates from the Prydz Bay region were surveyed, during January and February 1993, by the Museum of Victoria in conjunction with the Australian Antarctic Division. The study region comprised Prydz Bay (70–80°E) and the MacRobertson Shelf (60–70°E), south of the Kerguelen Plateau in eastern Antarctica. One of 36 holothurian species recorded from this survey, was determined to be a new species of *Myriotrochus* and is described herein.

The single specimen is damaged and consists of the anterior part of the body. Although a complete morphological and anatomical description is not possible, the critical taxonomic characters, including the form of the ossicles and the calcareous ring, are present and described and clearly differentiate the new species from others of the genus.

Order APODIDA Brandt, 1835

Family MYRIOTROCHIDAE Théel, 1877

Myriotrochus antarcticus sp. nov.

Myriotrochus sp. MoV 2039 O'Loughlin et al., 1994: 553, 554.

Fig. 1A–D

Material examined. Holotype (anterior part of the body). Eastern Antarctica, western MacRobertson Shelf (66°55.51'S, 62°32.27'E to 66°55.33'S, 62°32.16'E), 113 m, WHOI epibenthic sled, M. O'Loughlin on ANARE RSV *Aurora Australis*, 11 February 1993 (stn AA93-124), Museum of Victoria F69125 (with 1 slide).

Diagnosis. Tentacle ossicles absent. Pieces of the ventral part of the calcareous ring not significantly longer than those of the dorsal part; posterior

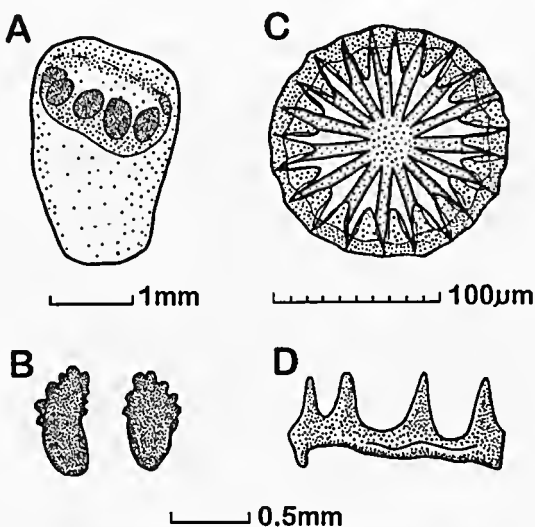


Fig. 1. *Myriotrochus antarcticus*, holotype, F69125. A, anterior part of the body. B, tentacle. C, wheel ossicle from the body wall. D, pieces of the calcareous ring, view through skin.

margin of the calcareous ring slightly undulating, not distinctly concave. Wheels 140–150 µm in diameter with 15–16 spokes and 22–24 teeth.

Description. Holotype: an anterior body fragment, 2 mm long, 1.3 mm in diameter (Fig. 1A). Skin translucent, colour in alcohol greyish-white. Tentacles 12, peltato-digitate, with 8–10 digits (Fig. 1B). Tentacle ossicles absent. Calcareous ring composed of 10 pieces; posterior margin slightly undulating, not distinctly concave; two dorsolateral radial pieces bearing two prominent anterior processes, remaining segments with a

single prominent anterior process (Fig. 1D). Pieces of the ventral part of the calcareous ring not significantly longer than those of the dorsal part. Two wheel ossicles were isolated from the body wall (Fig. 1C); their parameters are outlined in Table 1.

Wheel diameter (μm)	140	150
Number of spokes	15	16
Number of teeth	22	24
Spokes/teeth (%)	68.2	66.7
Hub diameter/wheel diameter (%)	18.6	18.0
Teeth length/wheel diameter (%)	18.6	18.0

Table 1. Wheel parameters in *Myriotrochus antarcticus*.

Etymology. This species is named for the locality from which it was collected, Antarctica.

Distribution. The species is known from a single specimen collected from the western MacRobertson Shelf, eastern Antarctica, 113 m.

Myriotrochus antarcticus is the first myriotrochid species to be recorded from the shelf in the Southern Hemisphere. All other shelf species of *Myriotrochus* are distributed in the Arctic (*M. eurycyclus*), the Arctic and northern parts of the Atlantic and Pacific (*M. rinkii*) and the northern Pacific (*M. mitsukurii*). In the Southern Hemisphere myriotrochid species have previously been recorded only from bathyal, abyssal and hadal depths (Belyaev & Mironov 1982).

Remarks. The genus *Myriotrochus* contains variably sized species. The diameter of the calcareous ring is commonly used as a size characteristic, as many reference specimens are contracted, or present in museum collections as body fragments. Some large species, such as *M. clarkei* or *M. giganteus* reach up to 11 or 12 mm in diameter, however most species are moderately sized and vary from 3–8 mm in diameter. One small species, *M. mitis*, reaches only 0.75–2 mm in diameter. However, size of wheels from the body wall does not necessarily correspond to body size. For example, *M. vitreus* reaches a diameter of 6 mm but average wheel size is less than 100 μm . Thus it is not possible to extrapolate the maximum body size of *M. antarcticus* or determine whether the specimen described herein may be a juvenile or adult specimen.

Below we compare the characteristics of the calcareous ring and body wall ossicles of *M. antarcticus*, with those of all other *Myriotrochus*

species. Wheels of corresponding sizes were compared interspecifically, where differential size data was available. The average wheel parameters *M. antarcticus* differ from those of all known species of the genus.

General comparison. *Myriotrochus eurycyclus* Heding, 1935 and *M. mitsukurii* Ohshima, 1915 differ from *M. antarcticus* by the presence of wheels in the tentacles (Heding 1935b; Ohshima 1915). *M. eurycyclus* also differs in the form of the calcareous ring which differs greatly in height in the dorsal and ventral aspects.

M. bathybius Clark, 1920 differs by the presence of wheels with a perforated hub, and by the conical and tapering tentacles rather than the peltato-digitate form exhibited by *M. antarcticus* (Clark, 1920).

M. clarkei Gage & Billet, 1986 and *M. vitreus* Sars, 1866 differ in the form of the calcareous ring, which differs greatly in height in the dorsal and ventral aspects and has prominent posterior processes, and by the conical and tapering tentacles (Heding 1935a; Gage & Billet 1986). *M. vitreus* also differs in having smaller sized wheels of 55–95 μm (Sars 1877; Østergren 1903). Although wheel diameters of 130–150 μm in *M. clarkei* are similar to those found in *M. antarcticus*, other wheel parameters differ (Gage & Billet 1986).

M. mitis Belyaev, 1970, *M. giganteus* Clark, 1920, *M. longissimus* Belyaev, 1970 and *M. macquoriensis* Belyaev & Mironov, 1981 all differ in having less prominent anterior processes on the segments of the calcareous ring. *M. mitis* also differs in the smaller wheels of 85–100 μm (Belyaev 1970). Although wheel diameters of 140–160 μm , in north-east Atlantic specimens *M. giganteus*, are similar to those found in *M. antarcticus*, spokes number 10–13 compared to 15–16 in *M. antarcticus* (Gage & Billet 1986, fig. 12). Similarly, wheel diameters of 120–160 μm in *M. longissimus* overlap the size of those found in *M. antarcticus*, however spokes average 9.9 in *M. longissimus* (Belyaev 1970, fig. 7). *M. macquoriensis* also differs in the form of the wheels which have an undulating margin, and a comparatively smaller wheel hub which averages 14–15% of the wheel diameter in *M. macquoriensis* compared to 18.0–18.6% in *M. antarcticus*.

M. rinkii Steenstrup, 1851 differs in some wheel parameters (see Belyaev & Mironov, 1982). In *M. rinkii* the wheels range in diameter from 130–280 μm , but average about 200 μm , compared to 140–150 μm in *M. antarcticus*. Hub diameter/wheel diameter ratio ranges from 7–16% with an

average of approximately 11% in *M. rinkii*, compared to 18.0–18.6% in *M. antarcticus*. In addition, the knob of the hub is more clearly distinguished in *M. rinkii* than in *M. antarcticus*.

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DIFFERENT ZOOPLANKTON COMMUNITIES IN CONFLUENT WATERS: COMPARISONS BETWEEN THREE MARINE BAYS IN VICTORIA, AUSTRALIA

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Zooplankton was collected from two sites in Swan Bay (adjacent to, and confluent with, Port Phillip Bay), Victoria, from February 1984 to January 1985. The copepod *Acartia tranteri* Bradford was numerically dominant throughout the year. The zooplankton assemblage in Swan Bay was more similar to that of the remote Westernport Bay than to the adjacent Port Phillip Bay. It is suggested that the presence of seagrass in Swan Bay and Westernport Bay had a strong, although indirect, influence on the nature of the zooplankton community by adding a significant amount of detritus to these systems and by providing habitat for small planktivorous fish.

DIFFERENCES in the zooplankton fauna of two closely situated bays, Port Phillip Bay and Westernport Bay (Fig. 1), have been attributed to their different physical and biological characteristics such as depth profiles, predator abundance, concentration of suspended matter and degree of tidal exchange with Bass Strait (Kimmerer & McKinnon 1985). For example, Westernport Bay is smaller and shallower and supports a very extensive eelgrass community (Robertson & Howard 1978), whereas Port Phillip Bay consists of a large, relatively deep basin with seagrass restricted to the shallow margin (Bulthuis et al. 1992). A consequence of this is that Westernport Bay may support a largely detritus-based ecosystem which has its energetic origins in the seagrass beds while the food web of Port Phillip Bay is more likely to be phytoplankton-based.

Swan Bay is located at the southern end of Port Phillip Bay (38°14'S, 144°40'E). It is a shallow, semi-enclosed body of water that covers an area of approximately 19 km² (Fig. 1). The maximum depth of Swan Bay is approximately 2.5 m. Two channels, one north and one south of Swan Island, provide limited tidal exchange with Port Phillip Bay. Intertidal mudbanks are common throughout the bay, and there is extensive coverage by seagrass; most commonly *Heterozostera tasmanica* (Denning et al. 1986).

Swan Bay is partially independent of, and different in character to, Port Phillip Bay, and so allows an extension to the comparative studies of Port Phillip Bay, Westernport Bay and Bass Strait undertaken previously (Kimmerer & McKinnon 1985). Although Swan Bay has direct tidal

exchange with Port Phillip Bay, it exhibits many characteristics closer to those of Westernport Bay, in particular, the presence of extensive seagrass beds. Thus, the area provides an opportunity to examine the factors that control a zooplankton assemblage. Does the species pool available for recruitment from Port Phillip Bay entirely dictate which organisms are able to live in Swan Bay, or is the assemblage determined by some combination of local biotic and abiotic factors?

The main objective of this study was to examine the zooplankton assemblage of Swan Bay and compare it to those of both Port Phillip Bay and Westernport Bay. The zooplankton in Swan Bay was sampled over a full year. The data were used to construct a species abundance curve that was compared to those from Port Phillip Bay, Westernport Bay and Bass Strait. Inferences were then made about the possible factors governing the species assemblage in Swan Bay.

MATERIALS AND METHODS

Zooplankton in Swan Bay was sampled monthly from February 1984 to January 1985 from two sites, one nearshore and one offshore (Fig. 1). At each site, four replicate samples were collected using a Clarke–Bumpus plankton sampler (mesh size 167 µm) that was towed for five minutes at a depth of one metre. Samples were collected during daylight hours at high tide. All samples were immediately preserved with 5% formaldehyde. In the laboratory, samples were fractionated so that between 500 and 800 individuals were counted for

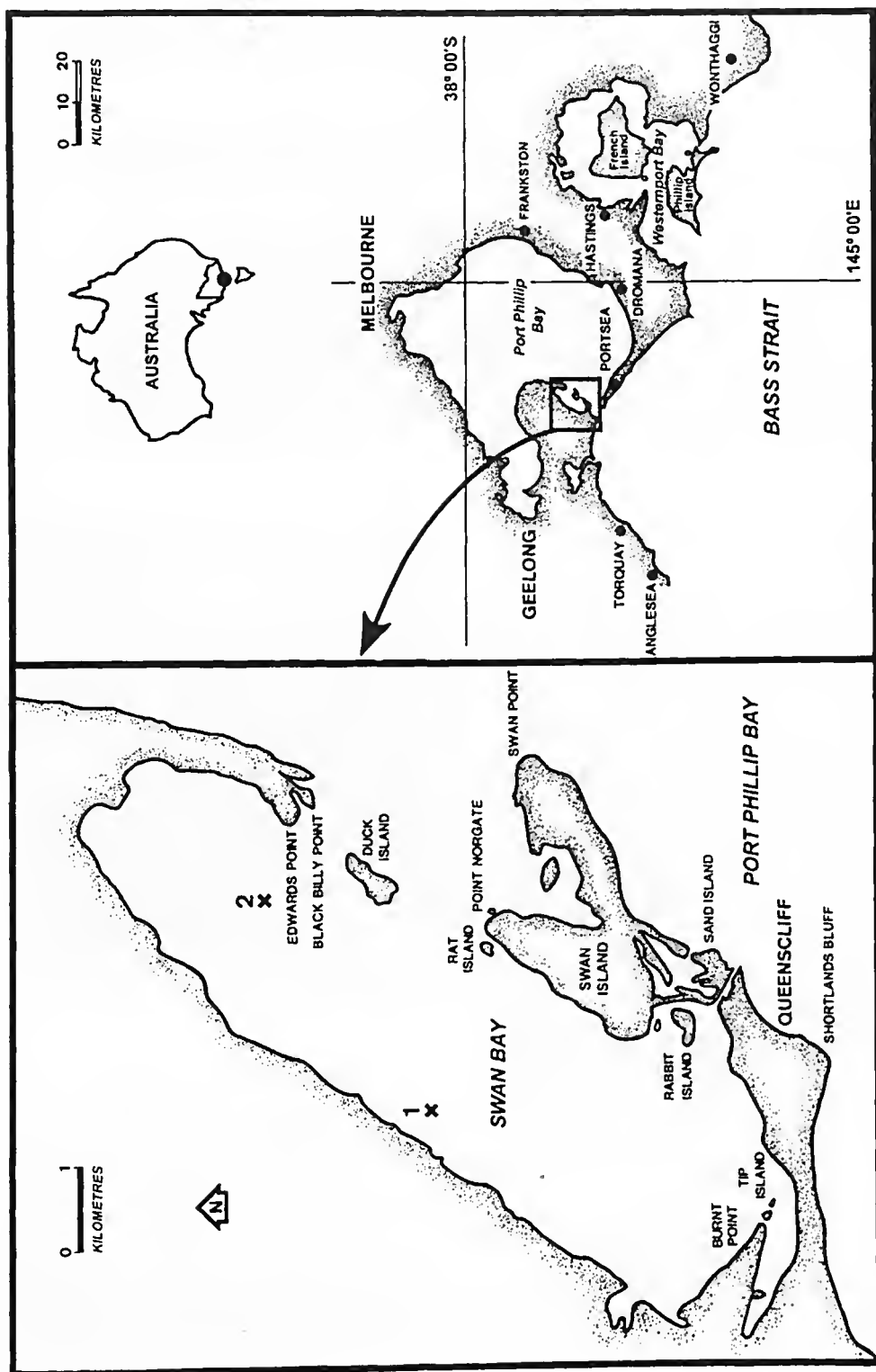


Fig. 1. Map showing location of Port Phillip Bay, Westernport Bay and Swan Bay. The location of the two sampling stations employed in Swan Bay is indicated by numerals 1 and 2.

each field replicate. Staining with rose bengal (Hellawell 1978) facilitated sorting when a large quantity of detritus was present. Zooplankton were identified to the lowest possible taxon. Geometric mean abundances were calculated using the transformed $\log(x+1)$ values (Sokal & Rohlf 1981). Student's *t*-test was used to test for differences between the mean zooplankton densities at each station.

On each sampling date, surface and bottom temperatures were measured using a mercury-in-glass thermometer. Water depth was measured with a graduated lead-line. Replicate mid-water samples (Van Dorn sampler) were collected for the determination of salinity using the conductivity ratio method (UNESCO 1966).

Phytoplankton samples were collected from mid-water depth using a Van Dorn sampler. Chlorophyll-*a* was extracted from the samples using the method of Nusch (1980). Absorbance was measured at 665 and 705 nm with a Varian-Techtron Spectrophotometer. Correction for phaeophytins was made by acidifying the extract with 3 μ L 2M HCl/mL, and remeasuring the absorbance after 15 minutes. From May 1984 replicate mid-water samples were collected to measure total suspended matter in the water column. Samples were filtered onto preweighed Oxoid membrane filters (0.45 μ m), dried at 60°C for four hours, cooled in a desiccator, and weighed to constant weight.

In order to characterise the distribution of species abundance in the zooplankton community of Swan Bay, a curve was constructed for the twelve most commonly occurring species; defined as those that were found to occur in more than one third of the samples. The $\log(x+1)$ abundance of each species was plotted against its rank, from the most frequently occurring species to the least. Comparisons were made to similar curves that had been developed for Port Phillip Bay, Westernport Bay and Bass Strait zooplankton communities (Kimmerer & McKinnon 1985).

RESULTS

Water depth ranged between 1.1 and 1.8 m at Station 1 and 1.8 and 2.5 m at Station 2. Surface seawater temperatures ranged between 9.8°C in June and 18.5°C in February. As expected for a shallow water column, thermal stratification was negligible; the maximum difference between surface and bottom temperatures was 0.3°C. Salinity varied between 33.1‰ in March and 39.6‰ in June.

Chlorophyll-*a* concentration ranged between 3.5 μ g L⁻¹ in February and 0.5 μ g L⁻¹ in April at Station 1 (mean=1.3 μ g L⁻¹) and between 2.2 μ g L⁻¹ in March and 0.3 μ g L⁻¹ in August (mean=0.9 μ g L⁻¹) at Station 2. Total suspended matter in the water column varied from 1.5 to 116.7 mg L⁻¹ at Station 1 and from 1.7 to 66.3 mg L⁻¹ at Station 2. There was no consistent seasonal trend; the amount of suspended matter appeared to be a function of prevailing weather conditions. Total suspended matter reached a maximum concentration in August when wind speeds reached at least 35 knots.

Geometric mean abundance of zooplankton reached a maximum (11 200 individuals m⁻³) in February and a minimum (570 individuals m⁻³) in July at Station 1 (Fig. 2). Mean abundance at Station 2 ranged from 1100 individuals m⁻³ in February to 220 individuals m⁻³ in June (Fig. 2). Mean densities at Station 1 were significantly greater than those at Station 2 (Student's *t*-test; *t*=3.434; d.f.=21; *P*<0.01). The zooplankton assemblage was dominated by Crustacea, particularly calanoid copepods. Other taxa represented included Mollusca, Leptomedusae, Chelicerata, and Polychaeta. In general, a greater number of taxa was collected at Station 2 but numerical abundances were usually considerably lower.

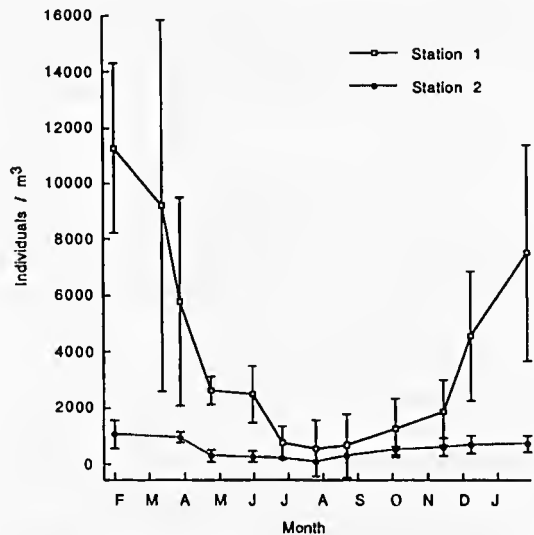


Fig. 2. Geometric mean zooplankton abundance at two stations in Swan Bay over the period February 1984 to January 1985.

	Station 1		Station 2	
	Mean	Range	Mean	Range
COPEPODA				
<i>Acartia tranteri</i>	3686	(509–11140)	611	(185–1668)
<i>Paracalanus indicus</i>	3	(1–19)	3	(1–11)
<i>Pseudodiaptomus cornutus</i>	47	(16–184)	9	(1–37)
Other Calanoida			1	(1–3)
<i>Oithona rigida</i>	48	(1–425)	36	(1–201)
<i>Oithona</i> sp.	27	(10–232)	28	(6–137)
<i>Kelleria corioensis</i>	7	(2–34)	5	(2–31)
<i>Metis</i> sp.	15	(6–68)	12	(1–64)
<i>Euterpina acutifrons</i>	2	(1–11)	2	(1–12)
Other Harpacticoida	7	(1–85)	1	(1–4)
OTHER TAXA				
Amphipoda	1	(1–9)	2	(1–4)
Isopoda	2	(4–19)	3	(1–15)
Decapoda	1	(2–3)	35	(1–10)
Mollusca	2	(1–16)	2	(1–8)
Polychaeta	1	(1–2)	4	(1–28)
Leptomedusae			7	(1–29)
Acariniidae	1	(1–2)		
Pisces	5	(2–50)	2	(1–8)

Table 1. Mean abundance (no. m^{-3}) of major taxa collected at each station over sampling period from February 1984 to January 1985. Range of abundances (minimum to maximum) shown in parentheses.

Acartia tranteri Bradford was numerically dominant throughout the sampling period at both stations, representing on average 82% of the total zooplankton numbers (Table 1). *Paracalanus indicus* Wolfenden, the most common calanoid copepod recorded from Port Phillip Bay (Arnott 1974b; Kimmerer & McKinnon 1985) was recorded in low numbers, the maximum abundance being $23 m^{-3}$ in March. The only other regularly recorded calanoid copepod was *Pseudodiaptomus cornutus* Nicholls. This is a benthopelagic species that migrates vertically (Fancett & Kimmerer 1985), and therefore was likely to be under-represented in daylight samples from Swan Bay.

The most abundant cyclopoid copepod, *Oithona rigida* Giesbrecht, was recorded most frequently from Station 2. However, when it was present, abundances were higher at Station 1. Low numbers of *Kelleria corioensis* Arnott & McKinnon and *Oithona* sp. were also recorded. *Euterpina acutifrons* Dana, a planktonic harpacticoid copepod, was collected throughout the sampling period, although generally in low numbers. Other harpacticoids occurred rarely and most likely

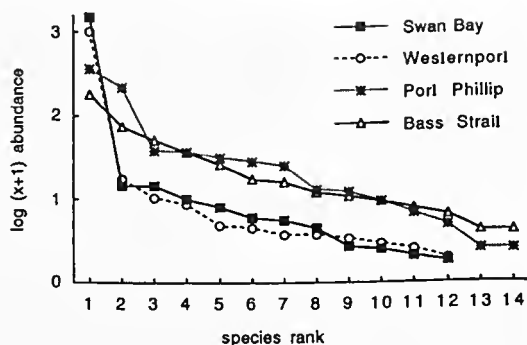


Fig. 3. Species abundance curves for Swan Bay, Westernport and Port Phillip Bays, and Bass Strait. Data for the last three localities from Kimmerer and McKinnon (1985).

represented benthic 'strays'. Amphipods, isopods and decapods were recorded from the stations occasionally and usually as the larval stages of benthic species. Other meroplanktonic organisms collected included trochophore larvae of polychaetes, mollusc larvae, pycnogonid larva (single specimen), acariniids and larval fish. The Leptomedusae, *Clytia hemispherica* and *Obelia* sp., were commonly collected from both stations.

Figure 3 shows log abundance plotted against species rank for Swan Bay, Westernport Bay, Port Phillip Bay and Bass Strait. Swan Bay was most similar to Westernport Bay in that the zooplankton assemblages were dominated by one species: *Acartia tranteri* in both cases. In terms of abundance, other species contributed relatively little to the total. In contrast, Swan Bay was dissimilar to Port Phillip Bay, which closely approximated Bass Strait in that there was not one predominant species but at least two that were contributing substantially to the total abundance. The two numerically abundant species in Port Phillip Bay were *A. tranteri* and *Paracalanus indicus* (Kimmerer & McKinnon 1985).

DISCUSSION

Comparison of the species abundance curves in Fig. 3 suggests abundance and distribution patterns of the Swan Bay zooplankton assemblage were much closer to those of Westernport Bay than to those of Port Phillip Bay, even though Swan Bay is hydraulically continuous with the latter. Unlike Port Phillip Bay, Swan Bay was strongly dominated by one species, *Acartia tranteri*. More-

over, *Paracalanus indicus*, a common species in Port Phillip Bay, was present only in low numbers in Swan Bay and other taxa which were all common in Port Phillip Bay, such as several species of cladocerans and larvaceans, were completely lacking in Swan Bay. Therefore it can be concluded that the broad hydraulic connection with Port Phillip Bay was only a minor factor affecting the species assemblage of Swan Bay.

Although the shallowness of Swan Bay suggests it was likely to experience wider short-term temperature fluctuations, the seawater temperatures during 1984 were not substantially different from those in the other two bays (Kimmerer & McKinnon 1985). Further, salinity values were similar for the three water bodies even though Swan Bay did become hypersaline during the winter (maximum salinity=39.6‰; c.f. 37.1‰ for Port Phillip Bay and 37.8‰ for Westernport Bay). Kimmerer & McKinnon (1985) concluded that temperature and salinity did not have a significant effect on the taxonomic differences they observed, and this study supports that conclusion.

High detrital levels in the water column may explain some of the differences observed. Large quantities of detritus found in Swan Bay (this study) and Westernport Bay (Arnott 1974a, 1974b) result from extensive seagrass coverage. Of those organisms commonly found in Port Phillip Bay but not in Swan Bay, for example *Paracalanus indicus*, some cladoceran species, and larvaceans, most are suspension feeders. These animals must either consume detritus, a comparatively poor food source, or actively take measures to reject it (Heinle et al. 1977). While some planktonic organisms are able to do this (e.g. Richman et al. 1977; Koehl & Strickler 1981), others, such as larvaceans, are unselective and so face difficulties with clogging of their incurrent filters (Alldredge 1976). In contrast, *Acartia* species are often numerically dominant in bays with high particulate content (Trinast 1975; Paffenhofer & Stearns 1988), and therefore must be able to tolerate detritus. Thus the high levels of detritus in Swan Bay might influence which species can successfully colonise the bay.

Phytoplankton abundance is partially limited by water temperatures and, in turn, limits zooplankton abundance. As chlorophyll-*a* concentrations (a measure of phytoplankton biomass) were consistently low in all three bays under consideration (Kimmerer & McKinnon 1985) when compared to values from temperate bays elsewhere (e.g. Durbin & Durbin 1981) it is unlikely that this factor alone was responsible for the observed differences.

Kimmerer & McKinnon (1987) showed that predation by small planktivorous fish on *P. indicus* was approximately twice that of predation on *A. tranteri*. They suggested that seagrass beds in shallow waters, such as those found in Westernport Bay, provide habitat for high numbers of small planktivores that are primarily visually oriented predators. In their study Kimmerer & McKinnon (1987) showed that *Acartia tranteri* was less visible in the water column and also had a greater ability to avoid capture than *P. indicus*. Their conclusion was that predation by fish had an important role in structuring the zooplankton assemblage of Westernport Bay. It is possible that such a mechanism is also operating in Swan Bay. The shallow waters and extensive seagrass beds do provide habitat for large numbers of small planktivorous fish (R. Jessop, personal communication, 1984). However, until predation pressure in Swan Bay can be quantified, its role in structuring the zooplankton assemblage will only be conjecture.

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NOMENCLATURAL NOTE

Narinia, a new name for the Permian brachymetopid trilobite genus *Iriania* Archbold 1981

Through the courtesy of Professor James X. Corgan (Austin Peay State University, Tennessee, USA) and Dr Larry W. Knox (Tennessee Technological University, Tennessee, USA), it has been pointed out that the generic name *Iriania* Archbold 1981 is a junior homonym of *Iriania* Diakonoff 1955, a genus of Lepidoptera from the island of New Guinea. In view of the subsequent use of *Iriania* Archbold 1981 by trilobite workers (Hahn & Hahn 1985), I therefore propose the new name *Narinia* to replace *Iriania* Archbold 1981 for the Permian trilobite genus. The etymology of *Narinia* is based on a rearrangement of the letters contained in the word *Iriania*.

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TRANSACTIONS
OF THE
ROYAL SOCIETY OF VICTORIA

OBITUARY—P. S. LANG

PATRICK SELLAR LANG, OBE (1980), BAGRSc, PhD (Melb.), HON.DSc (Deakin), FAIAS
22 July 1912–14 November 1996



Dr Patrick Sellar Lang

Dr Patrick Sellar Lang was a member of the Royal Society of Victoria from 1938 until his death at Camperdown, Victoria, on 14 November 1996.

Pat Lang was born in Melbourne on 22 July 1912 and was educated at Geelong Grammar and the University of Melbourne (Trinity College) where he graduated BAgrSc in 1934. As a student he won a Blue for Rifle Shooting. During 1937–38, he worked as a research assistant with Professor S. M. Wadham in the School of Agriculture at the University of Melbourne and, from 1939 until the end of World War II, he served in various army units. He was appointed second in command of the 2/5 Australian Independent Company (a commando unit) in 1942 with the rank of Captain and served in Papua New Guinea where he was Mentioned in Dispatches, promoted to Major and, after serving in other areas, awarded the Efficiency Medal.

After the War, he returned to the School of Agriculture and, until 1946, assisted Professor Wadham on the Rural Reconstruction Commission. As part of the School's research program, he was engaged from 1947–50 in a Survey of the Sheep Industry of the Western District of Victoria. For his work on this project, he was awarded a PhD by the University of Melbourne.

In 1950, he returned to live at the family's grazing property, 'Titanga'. He already had an amateur radio license (issued in 1948) and was one of the pioneers in the use of radio in the Rural Fire Brigade in which he maintained a deep interest for the rest of his life. He was Honorary Secretary of the Lismore RFB Group from 1951–90 and was the Group's Communications Officer from 1951 onwards. He was a Regional Delegate to the Victorian RFB Association from 1955–67 and President of its Central Council from 1970–73.

Pat Lang maintained a deep interest in the grazing industry, being a member of the Council of the Victorian Graziers' Association from 1956–73 and President from 1970–73. He was also a member of the Australian Woolgrowers' Council from 1968–73. He recognised the great importance of education to the community in general and to the farming community in particular. He was a member of the Council of Marcus Oldham Farm Management College (1966–95), a member of the Council of the Victorian Institute of Colleges (1968–70) and a member of the Universities Council of the Tertiary Education Commission (1977–83).

Not content with involvement in agriculture and education, he maintained a general interest in science and industry. He was a member of the CSIRO Victorian State Committee (1964–70), an Associate Commissioner of the Industries Assistance Commission (1975–76), a member of the Commonwealth Council for Rural Research and Extension (1978–81) and a member of the Australian Science and Technology Council (1979–82). He served on the Victorian Agricultural Engineering Advisory Group (1977–88) and was a member of the Advisory Group for the Australian Wool Harvesting Project (1977–82).

In addition to his professional activities, he found time to enjoy writing and two hobbies—amateur radio and palaeontology. Apart from scientific publications, he wrote two books—'Brown's Waterholes: A History of Lismore, 1840–1981' (jointly) and 'From Beater to Knapsack: History of the Lismore RFB Group'.

His community service was recognised by various honours. He was made a Fellow of the Australian Institute of Agricultural Science in 1970 for his outstanding contribution to agriculture and he was awarded (via the Country Fire Authority) the Queen's Long Service and Good Conduct medal in 1976. In 1980, he was made an Officer of the Order of the British Empire for his contributions to agriculture and education in Australia. He received an Hon.DSc from Deakin University in 1989 and, in 1992, was made an Honorary Life Member of the Country Fire Authority.

Pat Lang was a leader and a quiet, determined, hard-working, innovative, gentle man with a scientific mind and a good sense of humour. He was a superb example of how an educated person, far from the corridors of power, can have an important and beneficial influence in areas where he has good basic knowledge and experience. He will be missed, not only in the Lismore district, but by many friends scattered throughout Australia; we join in expressing deep sympathy to his wife, Nell, to their children Christopher and Andrew, and to their families.

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OBITUARY—J. H. WILLIS

JAMES HAMLYN WILLIS DSc (Melb.)

26 January 1910–10 November 1995

MAKER OF THE THIRD FLORA OF VICTORIA



Dr James Hamlyn Willis

I was one of the many friends of Dr Jim Willis who heard the sad news of his death in November 1995. We were both fascinated by the richness of the Australian flora (especially the small ground orchids) originating in our early days from family interest in bushland, for him, located in northwest Tasmania, and for me, in the drier gold mining soil of the St Arnaud countryside, Victoria.

We met first in 1938 at the University of Melbourne when he was a part-time student for BSc and I was into my third year of research training at the School of Agriculture, on the new pasture legume, subterranean clover (*Trifolium subterraneum*).

Keen to become a professional botanist, he had joined the taxonomic staff at the National Herbarium in October 1937, after nine years service with the Victorian Forests Commission, the first three years (1928–30) as an outstanding scholarship student at the Victorian School of Forestry, Creswick, and the next six years as a forestry officer.

At Creswick, encouraged by the Principal, Mr E. Semmons BSc, a fine biologist and teacher, he expanded his great interest in plants to fungi. He collected and studied the local fungi and the 'Bracket' group became the subject of his first published scientific article (in 1928!): 'Polyporaceae of the Creswick forest' (10 species). By 1930, he had noted 150 fungal species in the nearby forests and also collected and identified the vascular plants in that district and in the Grampians and Werribee Gorge.

By 1926, he had studied both plant and fungal species in five other forestry districts and had met Dr Ethel McLennan, the pioneer teacher of mycology and plant pathology in Victoria (Parbery 1989). In 1937, she was acting Head of the Botany School. News of impending retirements at the National Herbarium gave Willis his chance to transfer, spurred on by her urgent message to apply at once. Thus began his 34 years of distinguished service to that Institution and to Australia.

He was always a helpful colleague to us at the School of Agriculture, encouraging my use of the Herbarium Library and identifying puzzling grasses and other species. I could reciprocate occasionally with particular specimens such as lichens from Alaskan forests. Our common interest was genetic variation within the plant kingdom, my angle much more from an agricultural interest in the varieties of a species and his from the much wider one of species, genus, tribe and family.

I heard of course of his skills as a leader of botanical excursions within and outside Australia,

and also of his amazing memory for people as well as for plants. Much later on, after his retirement in 1972, I was able to admire his lecturing style first-hand at a Field Naturalists Meeting at Ballarat. We met for the last time as recently as August 1995 at the Royal Society's building, when Dr Nancy Millis gave her excellent lecture on Louis Pasteur.

Other friends have greatly expanded my knowledge of the breadth and depth of Jim Willis' personality and accomplishments (especially through the writing of Ann Latrielle and Leon Costermans), and I in turn would like to share my impressions of the problems and triumphs involved in the production of his academic masterpiece 'A Handbook to Plants in Victoria' (the third Flora).

PRELUDE

Why the need for a new Flora of Victoria? In 1927, the Victorian Government commissioned the Professor of Botany at the University of Melbourne (A. J. Ewart) to write the Second Flora. This was urgently needed to replace the first one ('Key to the system of Victorian plants') written by Dr F. Mueller, the first Government botanist, in 1888 (largely on behalf of the Field Naturalists Club, begun 1884).

In 1930, I was a first year botany student, and was told of the rewards that Professor Ewart had offered previous students for finding errors in the proofs of the then forthcoming Flora of Victoria, which was published in 1931. It was welcomed by many and my copy is still a prized possession. Over the following years, the teachers of plant taxonomy became increasingly dissatisfied as on-going research had made obsolete certain sections of that large and heavy book. This problem was reduced for a time by a class reference set of supplementary notes for the difficult sections. But the set was soon nicknamed 'The Monster' because of extra notes for other parts!

The pressure for an up-to-date authentic Flora increased steadily from year to year until 1939 when the outbreak of war diverted interest. Nevertheless, the plant scientists most concerned with the urgent need had begun to be hopeful because of the appointment of Willis to the Herbarium in 1937. They included Dr E. McLennan and the new Professor of Botany, John Turner (an English botanist already alerted to the ecological problems of soil erosion and the vanishing native flora, by his colleague S. M. Wadham, Professor of Agriculture 1926–56: Ashton and Ducker 1993) and the Director of the Herbarium and Botanic

Gardens, Mr A. W. Jessep BAGSC. They knew that the likely author had the desire, the skill and the energy to make a fresh survey of all the Victorian species and had already begun the collections. This foundation was essential but he would need special support (relief from routine responsibilities and adequate finance for extra staff) for the later stages of the project.

THE COMMISSIONING

In 1947, the Government of Victoria commissioned James J. Willis, now a Senior Botanist with an excellent record of fresh collections for the Herbarium (from 1937 onwards) and of critical research on the relationships of species and genera, to produce 'A Handbook to Plants in Victoria'. But post-war difficulties only provided partial support of the publishing cost and no extra finance otherwise.

However, due to the generous benefactor of the Botanic Gardens, Miss Maud Gibson, the necessary support and finance was made available. In response to Professor Turner's suggestion (the first Chairman of the Committee), the 'Maud Gibson Gardens Trust' sponsored this important botanical project by providing the salaries for temporary Herbarium assistants, and also the finance for journeys within Australia and overseas.

This enabled Willis to complete the essential field collections throughout Victoria. He also was appointed Australian Botanical Liaison Officer 1958–59 at the Royal Herbarium, Kew Gardens in order to study in England, the critical specimens from the historic visits of Banks and Solander with Captain Cook along the eastern coast of Australia (specimens at Kew Gardens and in the British Museum). In addition, he made lasting personal contacts with leading systematic botanists in other parts of the UK, in Europe and in the USA. On returning to Australia, he was then free, at least nominally, to undertake the essential literary work for the two volumes (Vol. 1 published 1962, 2nd edn 1970; Vol. 2, 1972). However, he was also Assistant Government Botanist from 1961 and acting Director of Herbarium and Botanic Gardens from October 1970 to January 1972!

THE MAKING OF THE HANDBOOK: PLAN

Inspired by Mueller's 'Key to the system of Victorian plants' ('an admirable handbook in its day'), Willis took up the challenge to write a similar 'Key' but on modern lines, combining all the surviving native species of vascular plants and the many established weeds of alien origin.

The scope of the project was enormous (precise, accurate information was needed for about 3000 species, including those within the 'Ferns and Conifers, and also those within the flowering plants—both Monocots and Dicots'). But the size of the book(s) must be small enough for field use.

The species would be accurately described and arranged in a form (an 'artificial' key) that enabled the interested student to identify a particular plant species easily in the field with its proper names (family, genus, species).

Each *species entry* would be standardised to provide the maximum essential information:

- i. the *preceding clues*: a pair of contrasting forms of a character along with several other contrasting reliable characters, derived from its particular structure and easy to see;
- ii. its *genus and species, original author and publication, place and date* (the citation);
- iii. references to *best illustrations*;
- iv. vernacular name;
- v. *Distribution* in Victoria and elsewhere;
- vi. extra notes where needed.

THE MAKING OF THE HANDBOOK: EVIDENCE

How did such a large project succeed? I was delighted to find the wealth of evidence in two sources: firstly, the two volumes of the Handbook (especially the Introductions) and secondly, the documents connected with his DSc (examiner's reports, selected special taxonomic papers and the list of his 700 publications up to 1971).

The Introductions: These revealed the complex nature of the project and the excellent level of planning, taxonomic skill, meticulous accuracy and teamwork needed to produce and assemble the necessary data for the book. For example, Willis made the thorough sampling of species and their distribution through the different vegetation provinces (natural regions) of Victoria (see fig. 1 in Anon 1975). But this material also had to be preserved and each species specimen identified by reference to the author's original description. The previous Herbarium collections by other people were also verified or corrected in the same way. Two helpers provided the list of accurate citations after months of checking the original descriptions by many visits to the Melbourne Public Library and by inquiries overseas. Two others listed the best illustrations and the Victorian localities represented by specimens in the Herbarium, one



Jim Willis with his wife Mavis (photo: B. Fuhrer, 16 September 1989)

produced the index for both volumes and a colleague from the Herbarium at Edinburgh in Scotland volunteered to mark the manuscript of Volume 1 for the guidance of the printers.

Willis constructed most of the keys from his vast personal knowledge gained from the surveys and listed for each species but gladly accepted some draft ones for some of the less familiar genera. He was fully responsible for the species entries, as well as for the presentation but also needed help with checking for errors throughout the progress from first draft to index and final proofs.

His acknowledgements reflect not only his appreciation of the special help of each of his 'several kindly, devoted team-workers in this onerous project' but also the tremendous support of his wife—'without whose unselfishness and cheerful encouragement he never could have completed his task'. 'Such gallant devotion is beyond all praise.'

The project took so long to complete (from 1947, about 25 years for the two volumes, including the second edition for Volume 1) that it must have been very difficult to keep to his high standard under the great pressure to finish: 'for unnamable nights over many years she remained

alone patiently controlling the home and family, while he worked with books and specimens at the Herbarium'.

On the other hand, there would have been many times of relief, even triumph, as difficult tasks were finished. One task involved learning to recognise the entire Victorian flora, section by section. In the complementary one, he had to design the keys for the groups of species within each genus and for the groups of genera within each family.

The Examiners' Reports: Both examiners agreed on the excellence of the Handbook as an up-to-date reference for both the professional taxonomist and the beginner. They especially praised the special value of the species citation (author and species: place of original reference) and the great increase of valuable data in a small space for each species compared with the same species in Ewart's Flora. They stressed that the concise, simple presentation masked the underlying basis of high academic achievement. However, this was clearly evident in Willis' sample group of scientific papers (part of his records of 50 new species) as well as in many others in the log list of publications.

IMPORTANCE OF AUTHOR AND HANDBOOK

Some 20 years after the Handbook was published, we can better appreciate the author's personal achievement, 'a milestone' (Aston 1996) in the growth of knowledge of Victorian plants, along the time-line from Mueller (1888) and Ewart (1931) to the Present. His teaching and taxonomic skills were crucial to the design and accurate content (including relevant research of others) of his two volumes. He thus provided a much clearer view of the botanical worth of the State than Ewart, both in terms of the diversity of species and genera and of their different habitats. His handbook, as forecast by the examiners, became an important factor ('the essential tool') in stimulating research groups in Victoria and elsewhere on systematic and ecological aspects of plant species.

In Victoria, much of this research had changed species names. As many professionals now need accurate up-to-date references, especially those concerned with plant conservation policies, the fourth Flora had to be urgently planned, a multi-author set of four large volumes. It was designed to attract a wider public by its layout and illustrations than was possible with the handbook style.

Willis had the pleasure of inspecting the first two volumes of the New Flora of Victoria. In Vol. 1 (1993) he was part-author of Chapter 5 (Botanical Exploration of Victoria). He also would have surely agreed with the editorial statement that only the surface of the essential botanical knowledge for plant understanding has been discovered so far. In Vol. 2 (1994) (Ferns, Conifers and Monocots) his data (Distribution and Ecology) was used in the species maps and his handbook praised for its continuing special use for field work.

THE MAN FOR THE TASK

Willis retired in January 1972, having successfully completed his very difficult commission begun in 1947. He was later persuaded to submit his scientific work to the University of Melbourne for the Doctor of Science Degree which was conferred on 24 August 1974. In retrospect, there is sufficient evidence of some of the personal factors involved in his early development as a botanical scientist to understand better the high quality of his achievements, especially the Handbook (see Conclusion).

Apprenticeship 1925–1937: Endowed with a fine intellect and a bent towards classifying the en-

trancing variation within the world of nature (mineral, vegetable, animal), Willis had the good fortune to be further encouraged towards biological enquiry during his early life. Firstly his father and his primary school teacher David L. Whitchurch helped in this way during his ten boyhood years in the wonderful coastal bush near Stanley, northwestern Tasmania.

Then in 1924, he moved to Victoria for his secondary education at Melbourne Boys High School and his brother in Launceston gave him at Christmas, Rodway's Tasmanian Flora (1903) which he soon learnt to use to identify for himself plants at home when on school holidays.

His tertiary training at Creswick (1928–30), provided his third and most important period of development, during which he made two special friends (his biology teacher and his future wife 'also a plant lover'), increased his skills and clarified his future aims.

As a first year student, Willis was unusually mature for his age (18) and had already expanded his Tasmanian interest in vascular plants to include those in Victoria. However, he responded eagerly to Mr Semmens' suggestion to study fungi 'that much neglected mycological section of the Plant World'. He thus found another life-long research interest based on taxonomy as well as the immense satisfaction of scientific discoveries in this new field. He (Mr Semmens) 'first led me to think seriously about our fungal gems, giving valuable aid in the beginner stage and whetting my passion to delve still deeper' (Willis 1941). In this book, Willis also thanked Dr E. I. McLennan 'for her courtesy and sympathetic help through many years in the determination of doubtful specimens' and Professor J. B. Cleland, MD, University of Adelaide, 'whose masterly treatise on South Australian fungi (1934) has resolved many of my problems'.

He also began his scientific writing as shown in his three student articles (Willis 1928, 1929, 1930) each a short but excellent survey. Each combined taxonomy and ecology (a lively concept at that time: Tansley 1926, 2nd edn) and stressed the immense scope of the topic for research. The first was on the Bracket fungi, already mentioned and the others on the broader associations of plant species in the complex locations at the Werribee Gorge and Creswick. The latter article (A Bird's Eye View of the Creswick Flora) is especially important because it gives a glimpse of his early fascination with making a 'census' (systematic arrangement) 'having lived at Creswick in constant touch with the native plants for nearly three years'. Note the inclusive

nature of that interest: flowering plants, ferns, higher fungi, lichens, mosses.

In addition, he made two important decisions, firstly to aim for professional botany rather than forestry (May 1996) and secondly, to follow his dream to make the best possible modern flora (for *field* reference) for Victorian vascular plants. At that time (1930), Mueller's 'Key' (1888) was still the only available one.

His next six years as a forester (1931–37) enabled him to increase his plant and fungi surveys of different forestry districts in Victoria and he also produced a major article on the Agaricaceae, or Gilled Fungi, of Victoria (Willis 1934). This was the best evidence at the time of his potential for his future Flora. It was 'a masterful work' (May 1996) composed from scattered references, much first-hand knowledge, excellent keys and description by word, line drawings and paintings of actual species (colour-plates and black-and-white photographs). It was later extended from 70–120 species (44 genera) in book form and became a general reference for schools and field naturalists for the next 50 years!

When he joined the National Herbarium in late 1937, he therefore had greatly increased his taxonomic skills from the first stage in 1925 (his use of the Tasmanian Flora) upwards towards the extraordinary level needed for his future Handbook.

CONCLUSION

Professor Turner composed the citation from Jim's Doctorate of Science from the examiner's assessment of his academic work of almost 40 years. He listed his accomplishments and traits as scientist and citizen as follows:

1. one of the leading plant taxonomists in Australia;
2. not only a world authority on the flowering plants of this continent but also with a high reputation in the fields as mosses and fungi;
3. not only a scholarly herbarium taxonomist of flowering plants, mosses and ferns, but also a first-rate botanist with unrivalled knowledge of the bush and the plants of Australia;
4. his scientific communications, an amazing range. His major work, the 1280-page, 2-volume *Handbook to Plants in Victoria*: clear evidence that he is a worthy successor to the great Baron von Mueller;
5. his traits: incredible industry and curiosity meticulous standard of work;

6. a man with great human qualities, never able to turn down requests for help (i.e. especially for community efforts to conserve our heritage of flora and fauna).

Although Willis had retired a little early (1972) his active life continues for over 20 more years, largely devoted to his widespread professional and community groups. In June 1995, he was made a Member of the Order of Australia, to honour his contribution to our nation as 'one of the great men of Australian botanical and natural history science'. 'He has given so much of his talent to so many ...' (Aston 1996).

We can also acknowledge, more simply his high calibre both as a scientist and as a caring family and community man; and be very thankful for his long life of joyful discoveries, infectious enthusiasm and generous sharing of his knowledge of our unique natural heritage.

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FIFTY YEARS A GEOLOGIST

EMERITUS PROFESSOR FRANCIS CLIFFORD BEAVIS
BSc(Hons) (Melb), PhD (Melb), MA (Cantab), LLB (UNSW), FGS

In February of this year (1997), Emeritus Professor Franc Beavis celebrated 50 years as a professional geologist. Educated at Echuca High School, Victoria, Franc had the good fortune to have as his headmaster, the distinguished palaeontologist Dr W. J. Harris, who introduced him to geology, and imparted a life long interest in graptolites. On matriculation to the University of Melbourne with a Senior Government Scholarship and the major residential scholarship to Queen's College, Franc quietly absorbed himself in study, with an occasional outburst of (restrained) student antics, and graduated BSc with majors in Geology and Mathematics.

His first professional appointment was as temporary assistant field geologist with the Geological Survey of Victoria on 12 February 1947, and was posted to the Bendigo office to assist in the remapping of the Bendigo Goldfields. In November 1947 he was transferred, on loan to the State Electricity Commission of Victoria, to the Kiewa Project as Geologist, with formal appointment to the SEC in 1949. This saw the beginning of a career in engineering geology as Franc was responsible for the regional mapping of the area as well as detailed geological studies for major dams, tunnels and underground power stations at Kiewa. Geological mapping was often done as sorties out from camp on horseback (the horse was in the habit of 'throwing', and always seemed to have an ear out for the 'knock off' whistle, when it would canter back to camp with or without rider) and involved extended periods of solitary work in areas of immense beauty but with unpredictable weather.

In 1952, Franc was appointed Geologist, in the Civil Engineers Branch of the SEC and carried out studies on the geology of foundations for surface thermal power stations at Yallourn, associated tunnels, and the Latrobe River Dam at Yallourn including pioneering work on brown coal as a foundation rock.

After 10 years in the SEC, Professor E. S. Hills offered Franc a lectureship in Geology at the University of Melbourne, and in the same year he was promoted to Senior Lecturer. In this position he developed courses in geology for civil and mechanical engineering student. L agricultural geology and structural geology. A much loved teacher, final year Agricultural Science students would present him with ever more adventurous

Christmas gifts each year including a number of farmyard animals. In 1961 Franc completed his PhD thesis at the University of Melbourne 'Geology of the Kiewa Area with Particular Reference to Structure', and in 1972 was admitted to the degree of Master of Arts, Cambridge.

In 1973, he was appointed to the Foundation Chair of Engineering Geology at the University of New South Wales where he developed with Dr (now Professor) Michael Knight, a strong post graduate department in engineering and environmental geology and hydrogeology. He was Head of the School of Applied Geology from 1973-1979 and again in 1982. During this time he completed his Bachelor of Laws at the University of NSW and was awarded the Stephen Jacques Prize in Constitutional Law.

He retired from academia in 1986 and moved to the relative calm of country life in Cowra, New South Wales where he practiced law as a barrister, lectured at Charles Sturt University in the Law Faculty, and developed a private consulting practice in geology. He subsequently relinquished his legal practice after a number of years on the grounds that clients, unlike rocks, are most unreliable witnesses of the truth. He is currently working on geological aspects of land degradation for Landcare groups in midwestern New South Wales.

Franc's research has covered three main areas: engineering geology, structural geology and palaeontology (graptolites). His most significant publication of a total of some 60 papers include 'The geology of the Kiewa Area' (published in the Proceedings of the Royal Society of Victoria); 'The Victorian Isograptids and Isograptid like graptolites' (co-authored with daughter Sara, in the Proceedings of the Royal Society of Victoria); a series of papers on the weathering of rocks in arid zones and the significance of arid zone water storages; and the monograph 'Engineering Geology' (published by Blackwell Scientific, 1985) and translated into Malaysian as 'Geologi Kjuruteraan' with an Iranian translation (currently in press).

He is a foundation member of the Victorian Division of the Geological Society of Australia and Divisional Secretary for several years; Member of the Royal Society of NSW (President 1978) and Fellow of the Geological Society of London. It is somewhat noteworthy that the entire Beavis family

comprising Frane, his wife Joan, and children Adrian and Sara are all members of the Royal Society of Victoria, with Frane's membership dating back to 1957.

Frane is known to his many colleagues, past students and friends as a remarkable scholar, gentleman and teacher whose distinguished career is a statement of his commitment to the profession.

When asked when he will retire, his response is 'An old geologist never hangs up his hammer!'.

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ROYAL SOCIETY OF VICTORIA
1997 J. E. CUMMINS ORATION

29 April 1997

Delivered by MR CHARLES ALLEN AO

SCIENCE, THE KEY TO AUSTRALIA'S FUTURE?

Professor Herbert Bolotin, President of the Royal Society of Victoria, Ladies and Gentlemen,

It is a great honour to deliver the 1997 J. E. Cummins Memorial Lecture and join a distinguished list of Orators beginning with Sir Louis Matheson in 1974.

The Royal Society of Victoria is to be congratulated for continuing the tradition of the Oration, begun in the Sciences Club that has since merged with the Society. Traditions remind us of our past, recognise our inheritance and provide us a path to the future. We do well to respect them. We must all contend with change, but we also need a frame of reference to manage that change and give it direction rather than be at its mercy. Our traditions and Institutions provide that frame of reference and their importance will be a recurring theme in my talk tonight.

The topic of my talk is 'Science, the key to Australia's future?'. This is not a statement, but a question, as you may have noticed in the program. I deliberately included the question mark when choosing the title for this talk.

When I am talking to a group of businessmen or to a general audience, I am very happy to be a champion of science. However, when talking to the Royal Society of Victoria, I am, by and large, talking to the converted. For that reason, I would like to take a different approach tonight. I would not presume to consider myself a scientist, but in taking on the job of Chairman of CSIRO, I have become part of the scientific community. Tonight, it is from the perspective of a member of that community, that I would like to discuss the current political and economic environment in Australia and critically assess whether Australian science does have a role in Australia's future.

In doing this, I will argue that it is not enough for us in the scientific community simply to point to the undoubted power of technological advance of this century to claim a position of privilege for Australian scientists. Like all Australians, we must earn our position and define a role and rationale that justifies the support we seek. We must do this because the brutal realities facing Australia in the global marketplace are such that Governments cannot and should not deprive one sector of the community in order to support another, unless there

is a clear national purpose in doing so—be that purpose economic, environmental, social, cultural or even, as was common to invoke one hundred and fifty years ago, Divine.

J. E. Cummins, whom we honour tonight, understood this I believe and was probably ahead of his time. Jack Cummins, as he was known, had a vision for furthering the cause of science. He went out and persuaded others that it was a vision worth supporting and was thus able to bring the National Science Centre into existence. The building, Clunies Ross House, may be no more, but the ideals on which it was founded continue within the merged Sciences Club and the Royal Society of Victoria.

When I read of Jack's achievements, I was struck by his desire to promote exchange between the different disciplines of science. The National Science Centre was intended to house the growing number of scientific, technological and learned societies together and promote exchanges between them. He perceived, from an early time, the importance of the interchange of ideas between scientists who were diverging into ever narrower fields of specialisation; he realised that debate, interaction and the cross fertilisation of ideas between scientists has been as much a driver of scientific advance as individual genius.

We cannot programme for individual genius—despite the recent birth of Dolly, the cloned sheep. But we can foster a climate of debate and interaction in which good science will prosper and occasional genius emerge. This is what Jack was trying to do with the National Science Centre and his vision remains highly relevant to us today, even if circumstances now demand a different approach.

To understand where science fits in modern Australia, it is necessary to understand the imperatives that are driving our nation. We are now part of the global marketplace. It is not coming—it is here. Modern telecommunications mean that no one can opt out of the marketplace—as the old Soviet empire discovered, too late. Attempting to opt out is like saying 'stop the world, I want to get off'.

Australia has no option but to compete in order to generate the wealth that will enable us to pay for the lifestyle we want—and I don't just mean our material well-being. There is no doubt that the wealthier a society, the better able it is to pay for maintaining a quality environment and providing a social welfare safety net for those in our community who deserve assistance and support. It's no accident that environmental protection and social welfare are low on the agendas of the poorer nations of this planet.

To compete in the global marketplace, we have to play from our strengths, but what are those strengths?

Or, adopting the jargon of the current industry debate, if we flattened the earth into a level playing field, where would Australia have 'bumps' of natural advantage?

The well known industry 'bumps' are in agriculture and mining, with perhaps marine industries on the horizon. As is well known, agriculture and mining have long supported Australia, giving us one of the highest standards of living in the world. In the case of agriculture, there are those who say that we have no natural advantage other than size. Be that as it may, the wealth generated in these two sectors was enough to support, until recently, a small, highly protected manufacturing and service sector.

But the changing patterns of world trade, in particular the entry of Britain into the Common Market, altered the outlook for Australia. The tigers of East and South-East Asia expanded rapidly through the '60s and '70s shifting the direction of our trade from Europe to Asia. But not only the direction of trade changed. So did its composition. The largest areas of trade growth were no longer in primary produce, but in manufactured goods, telecommunications and the information and service sectors.

Australia has few natural advantages in these sectors. We do not have a large domestic market in which to nurture producers. Our existing industries in these sectors were uncompetitive from years of cosy protection. And we had little experience in the new markets of Asia into which we now had to sell.

All this makes the 'flat earth' surrounding Australia look decidedly scorched! Not surprisingly, we've been scouring around to find a few more 'bumps' on which we can perch to catch a cool breeze.

Some people have suggested that we should use tariffs again to protect us from the ravages of this desert. That unfortunately is akin to the ostrich burying its head in the sand. The fact is that our

efficient agriculture and mining industries can simply no longer afford to carry those sectors the way they once did. For Australia to remain among the developed nations of this world, those sectors alone will not generate the wealth we need.

And I say this as someone who spent 16 years as the Managing Director of Woodside Petroleum Ltd which was the operating company for one of the world's giant projects, the North West Shelf Gas Project, involving an investment of some \$12 000 million over 15 years. This project alone generates over 1% of GDP and has created some 70 000 jobs throughout Australia. I am still excited by that project and the massive developments taking place in the resource developments in north-west Australia. But I also know that they, alone, will not carry our nation to the future to which it aspires.

I am not arguing that we should necessarily drop all tariffs to zero. Some nations would be happy to dump goods into Australia, destroy our industries and then sell us goods at a much higher price when the local competition is gone. This is the equivalent of a large company undercutting rivals until they are out of business so that they can then have the market to themselves. But that is a tactical issue. In the long term, tariffs are a cost to our economy that harm our ability to compete in other sectors and ultimately are paid for by the average Australian. Other countries may use tariffs, to distort the 'level playing field', but in doing so, they will not distort it permanently in their favour.

What we need, I suggest, is a more analytical way of doing things. We need to think of where our advantages lie, where we stand out as a hill on that flat plane. And we do not have to confine ourselves to those advantages coming from our endowment of agricultural land, resources and the marine sector. Indeed, we have more advantages than is commonly recognised.

One of our strengths which is often under appreciated is our Institutional structure. I'm talking here about our law, our constitution, our government, our educational system, the fact that our culture is predominantly ethical, where business can be done at a sensible, arm's length basis, and that our language is English, the international language of business. I have done business in many countries of the world and I have no doubt that these features are a great advantage to this country. They can make us a preferred location for many business activities.

Most people in Australia seem to take these for granted without appreciating the depth of experience and wisdom underpinning them. We

may be a young country on the southern edge of the globe, but the Institutions which form the basis of our Society are part of the continuum of a thousand years. Churchill wrote that '... a nation which has forgotten its past has no future'. Our past includes the history of those who established the nation's Institutional structure. As Arthur Bryant wrote 'In a democratic age, when the welfare and safety of society depend on the many, the cumulative guidance of the past and its inherited corporate experience is almost totally lacking. For the instinctive wisdom of the ages is a truer guide than the conflicting opinions of individuals, however clever.'

We need, therefore, to be very careful with our Institutions. By all means subject them to scrutiny and occasional review, but recognise them as an asset not cheaply to be discarded.

Our constitution is one such asset, presently the subject of much discussion, primarily focused around whether we should have an Australian head of state or retain the monarchy. For most people in Australia, this is the key issue. But others wish to see a much wider review of the Constitution, making fundamental changes. It may be that the monarchy/non-monarchy issue should be resolved first and in isolation from any other complications, since that one issue will be difficult enough. Clever people may believe that other changes are needed and hope to slip them all by as part of a package. But I am with Bryant in preferring a thousand years of experience to the cleverness of individuals.

I have expanded on this theme, which may seem a diversion from the topic of science. But I believe that we must understand our roots before we can consider how to use our science and industry to create our future. Our constitution and its stability has been part of the Institutional 'hill' on which our past welfare has been based and on which our future welfare can be founded. We should be very careful about altering it and I will not tonight be offering a view on what solution might be chosen. But I do note that Canada is a country that has spent a great deal of time and effort over the past twenty years discussing its Constitution and has little to show for it but a severe detriment to its economy and loss of welfare for its people.

Apart from our Institutions, we have a number of other very tangible strengths on which to build this nation's future. Our infrastructure is one such advantage. Many of the countries of Asia are struggling to maintain or even build the infrastructure they need for development. Cities are choked by traffic and roads and telecom-

munications are stretched to the limit. These make doing business much harder in those countries than in Australia. We, in Australia should need to spend a lesser part of our earnings on infrastructure. That does not mean however that we should rest on our infrastructure laurels and there is a grave danger of failing to maintain and constantly improve it, but it does put us ahead of many of our competitors.

Even more important is our intellectual infrastructure, and this is where our science comes in. Science may have a cultural aspect to it, but if it is to be part of the mainstream of our society, then it must be linked to the key imperatives of our nation, and none is more imperative than our competitiveness.

Knowledge and its application have long been a wellspring of comparative advantage. I recently read an interesting account of Samuel Peyps, who was Secretary of British Admiralty in the 17th Century. Peyps was a well educated man, a scholar at Cambridge, intelligent and curious. The British Navy was in the throes of a massive expansion as Britain rose to be the greatest sea power the world had ever seen. Peyps was responsible for much of this expansion and suspected that the Navy was being ripped off by contractors who were building and supplying this new navy—the world has, you see, not changed in all that many ways!

To understand the claims of the contractors, Peyps realised that he needed to learn arithmetic so that he could check on the accounts being submitted. This arithmetic simply consisted of adding, subtracting, multiplying and dividing, yet it proved a struggle for Peyps, involving monumental labour, dogged persistence and immense discipline on his part.

Now, you and I might wonder why someone so well-educated as Samuel Peyps would have such a difficulty with simple arithmetic, which today is child's play. The reason becomes clear with a little reflection: like all educated men of the time, Peyps had been taught only Roman numerals. If you have ever tried to multiply or divide with Roman numerals, you will understand that Peyps' difficulty did not stem from an intellectual incapacity for mathematics—the deficiency was in the system of knowledge he was using.

The contractors with whom the Navy was dealing, on the other hand, were all familiar with Arabic numbers and had no difficulty in calculating the costs of contracts. This gave them a real competitive advantage over the Secretary to the Admiralty and his clerks.

The account I was reading was fictionalised history, though Peyps was a real and remarkable fellow. Faction is how it is referred to. Whatever it is, it has an important message. Firstly, it underscores the enormous step forward the Arabic world made by its numerals, which made arithmetic and simple mathematics much easier to do. Secondly, it shows the enormous competitive advantage that education in the tools of the future can confer. I think that the modern day equivalent of the advantage coming from the Arabic numbers may well be the computer systems based on binary codes. No business can be without the power that these new systems deliver and any nation whose citizens are unable to use the systems based on these codes are at enormous competitive disadvantage to the rest of the world.

Clearly then knowledge can be a source of competitive advantage. And since science is really ordered knowledge, it is an obvious candidate from which we should seek competitive advantage. And indeed, Australia has a great tradition of using its science in its areas of natural advantage to make those hills nudge higher.

A good example is in the field of mineral exploration. CSIRO scientists developed an understanding of the formation of volcanic rocks that contain nickel in the Agnew-Wiluna Greenstone Belt in Western Australia. This fundamental science enabled them to predict the areas where nickel is most likely to be found. Using this knowledge, they worked with companies such as Dominion Resources to devise new exploration strategies and contributed to the discovery of major new nickel deposits in a region that had been explored for 20 years without success.

Similarly, CSIRO has developed exploration techniques for gold, suited to the unique Australian environment. These techniques directly assisted Great Central Mines in the discovery of the major Plutonic and Bronzewing gold deposits in Western Australia now being developed and earning valuable export income for their owners and for Australia.

We have also used science to increase our advantage in adding value to our primary produce. Australia has become the world's largest exporter of aluminium. It has done so not only using its natural advantages of vast coal and bauxite deposits, but through its science. CSIRO has worked with producers both individually and in consortia to address a range of fundamental issues in the production of alumina from bauxite.

We are hoping to do the same to give Australia a strong position in the rapidly growing market for magnesium. This metal has great potential

for the production of light-weight alloys for the automotive and aerospace industries. Australia has the largest deposit of magnesite in the world at Kunwarara, near Rockhampton. We are working with the owners of the deposit, Queensland Metals, to develop processes for the refinement of the ore to magnesium chloride and from there to high grade magnesium metal. This would increase the value of the ore up to 10-fold.

We are also seeking to go one step further and start fabricating magnesium alloy parts for both the aerospace and automotive industries, adding even further value to this resource. The decision by the Ford Motor Company to invest in a pilot magnesium smelter at Kunwarara is a very positive step to this end. Our Division of Manufacturing Technology has done a great deal of work on diecasting of such alloys and is undertaking fundamental research on alloy performance to give us an edge in this field. CSIRO is supplying eight magnesium alloy parts for the engine bay of Ford's new PT2000 demonstration car, including the engine mounts. The PT2000 project aims to cut car weight by 40%, without reducing performance. A lighter car means better fuel efficiency and both economic and environmental gains.

In agriculture, we have pressed our advantage through a long history of innovations. As many of you would know, CSIRO was founded on the vision of some of our earliest politicians—people such as Sir Billy Morris Hughes—who wanted to make the desert bloom.

I don't know that we've done that—we've still got an awful lot of bloom in desert!

But there have certainly been some stunning successes and huge areas of arid country have been brought into profitable production. Some recent successes have included the work CSIRO did to help make Australian vineyards among the world's most efficient, underpinning the explosion of Australian wine exports—a very high value added commodity.

The cattle tick vaccine developed by CSIRO in conjunction with Biotechnology Australia is another recent advance. It has a double benefit for Australia: it will improve the productivity of our beef herds in northern Australia by reducing the impact of the cattle tick scourge that currently costs the industry \$100 million annually; and the vaccine itself is a potential export to other nations. Coupled with better productivity in agriculture has been research into salinity and the management of discharges from sprayed agricultural areas to neutralise pesticide run-off.

I mentioned the marine sector as a potential

area of Australian advantage. Australia has the third largest area of ocean in the world in its Exclusive Economic Zone, an area about one and a half times its land area. This is an extraordinary resource, which is both an opportunity and a challenge. To date, fishing, offshore oil and mineral developments plus tourism are contributing to the value of this asset, but unfortunately, we have a lamentable lack of knowledge of this resource.

We have taken but a few steps toward its sustainable management, such as CSIRO's work on monitoring the bluefin tuna and in helping manage the Northern Prawn Fishery. The prawn fishery, in particular, is a model for fishery management. We have developed an understanding of the factors that cause the fishery to fluctuate, enabling spawning times and the size of the harvestable catch to be predicted. This has enabled the industry to avoid population crashes from over-fishing, while the models have also enabled them to minimise operational costs and enhance the quality of their catch. However, this is but a drop in the ocean of the total Australian marine resource.

The Government's recent allocation of \$106 million to marine studies is an important step toward developing our competitive advantage in marine industries. It will be needed not only to exploit the resources I've mentioned, but also to manage them for the enjoyment of Australians, whose love affair with the surf and sun still leads us to cluster on the coastal fringe. There is an urgency in these studies as we could yet lose our exclusivity to the EEZ if we have not shown that we have carried out sufficient studies on it.

If Australian science can help us to make more of our natural hills on the flat earth of the global marketplace, the obvious question is can it not make hills in its own right? In the age where intellectual property is becoming more important than physical property, can we use it to create a successful industry?

There can be no doubt that some countries have achieved this. Silicon Valley in California and the Cambridge phenomenon show that industries can be founded on ideas. A similar situation has arisen in India, which at first thought may seem improbable. I was interested to read recently that Bill Gates of Microsoft is investing in Bangalore, the home of the Indian air force training school, which is a flow on from establishments set up by the British in colonial times. The legacy of these establishments and the presence of the school seems to have imbued the people of Bangalore with a commitment to learning. The city has

nurtured a young, intelligent, well educated, English speaking workforce that has emerged as a highly competitive source of computer programmers. It is a service export that companies the world over are taking up, and Bangalore has become the computer capital of India.

Professor Michael Porter showed that the successful 'intellectual hills' were clusters of centres of excellence together with highly competitive companies. A reflection on some of the successful areas of Australian science, where we have built on our natural advantages show a similar structure—in mining we have highly competitive companies such as BHP, CRA, Western Mining and so on. We have excellent scientists within those companies, in the universities and in CSIRO who interact through the Australian Mining Industry Research Association to make Australia one of the world centres of excellence in the geological sciences.

Similarly in agriculture, we have developed centres of research excellence linked to a farming community that is competitive and committed to employing the results of the research. The wine industry I mentioned earlier is a case in point, developing from humble origins in the space of a couple of decades.

But what of the areas where Australia doesn't have such a clearly defined natural advantage on which to build. Do we have any equivalents of the Bangalore programmers?

Not surprisingly, while the Australian economy was largely protected, none emerged outside agriculture and mining. That may be an important factor in Australia's comparatively low levels of private sector spending on R&D. Our public sector spending is comparable to other OECD countries but our private sector expenditure is low, which means that the lion's share of future growth in Australian science must come from the private sector.

Since the reform of the Australian economy began there are signs of a few clusters with great promise. The most promising one is based around Melbourne's famed Parkville strip. There is the progress toward the new influenza drug based on the work of Peter Coleman's CSIRO Division of Biomolecular Engineering and others. There is the work of people like Don Metcalfe at the Walter and Eliza Hall Institute on factors that stimulate blood cells. This and other exciting research could help lay the basis of a competitive pharmaceutical industry in Australia. Already companies like the recently privatised CSL, AMRAD and Glaxo Australia are providing the essential commercial focus.

There are a number of other clusters with potential, such as the diecasting work for automotive parts that I mentioned earlier. The nucleus of clusters can also be seen in some of the successful Cooperative Research Centres, that have clustered industry and public researchers together. One of particular interest is in environmental management. There is no doubt that along with our successes in developing this country there have been some mistakes and in some areas our environment has suffered. Fortunately, the investment by Government and the private sector in conserving the fragile Australian environment is beginning to be exploited as an export of expertise, equipment and software. The suite of software for processing remote sensing images developed by CSIRO and now being marketed world-wide by Clough Engineering is a good example. They enable land use to be planned by farmers, miners and other developers on the basis of satellite images that can give early warning of stress, while monitoring vegetation, moisture and other environmental factors.

When thinking about these clusters, we also shouldn't allow our nationalism to get in the way of opportunities. The global marketplace means that even in the development phase, we should not place too much emphasis on national borders. Our position in a different time zone from centres of research and commerce is often seen as a major drawback. But, as always, problems can also be opportunities.

When working the North-West Shelf project, we were able to have the financing for Woodside's loan proceeding on a 24-hour basis. Work done in Australia was passed to the UK at the end of the day, which was the start of their day. When their working day ended, they could send comments and developments for those in Australia to pick up and take forward, so that the work was almost continuous. With modern communication technologies and electronic document transfer, the potential for active links with people outside our time zones can be turned into a commercial advantage not only in financing but in all aspects of project design provided outstanding communications exist between the centres. The opportunities which this gives for speeding up project developments are very exciting and is currently being progressed by the CSIRO START project which is focussing on a global concurrent engineering platform for teams working on software development in Europe, Australia and North America on a 24-hour basis.

What this all tells us is that we have a lot more reason to be optimistic about Australia's future in

a 'flat earth' marketplace than we might have thought at first sight. And science is an integral part of that optimism.

But before we get carried away and give a resounding yes to the question I posed at the outset—Science, the key to Australia's future?—we had better remember that there are a few caveats that go along with this.

One of the things that stand out in the examples I've given you is that the application of science requires dynamic, internationally competitive private sector involvement. Science on its own won't do anything for Australia's future other than perhaps some cultural enrichment. Worthy though cultural pursuits may be in their own right, they will not in themselves keep Australia among the advanced nations of this world, wealthy enough to support a rich culture.

Enhancing Australia's future through science requires a commitment to the continuing reform of Australia's economy and industry. I say this in the knowledge that the structural changes in the Australian economy have not been without pain. But Australia has much further to go, lagging behind progress in some countries. New Zealand is clearly nearly a decade ahead of us (although it may now be falling back) and the United Kingdom has also exceeded Australia's metamorphosis from Government companies to privatised ones. At the present time, there is concern in the private sector that the will to continue these changes has abated. But we must press on. Unemployment in Australia will not come down until reforms are implemented.

We also need the right macro-economic environment. Low inflation is essential to the pursuit of science in Australia. Inflation shortens the time horizons of business managers, which is a death knell for the investments in the years of effort required to turn research into marketable products. For similar reasons, interest rates need to be brought down.

Now, you might say that all that is for the politicians to sort out. But I'm afraid that's not good enough. We here tonight all have an interest in the outcome both as Australians and as part of the scientific community. If we want to be able to affirm that science will be the key to Australia's future, then these are some of the pre-conditions. We will not see the competitive companies emerging that can cluster with our centres of scientific excellence if the economic policy settings aren't right.

As I said at the outset, it's not enough for us simply to point at the power of technology. We have to show that we can use it to the benefit of

the nation and be aware of all the ingredients needed for success. We must not, as I believe has happened in the past, make claims that cannot be fulfilled. If we do, we are guilty of the special pleading by interest groups that have bedevilled our national progress for too long.

But if all this sounds a bit daunting, the good news for Australian science is that it shifts some of the pressure for change away from the scientific establishment. CSIRO and the Universities are not here to do industry's research for them. They provide a base of scientific knowledge on which Australians in industry, or working in other areas of national interest, can call upon when needed, a base which they could not afford on their own or find in many other countries in our region.

I think that in the past decade, erroneously, too much pressure has been placed on the scientific Institutions to change without creating the climate for a responsive industry. Both the Minister and the current Board of CSIRO believe that the Organisation now needs a period of stability, so that the focus of CSIRO can be on producing the results from its strategic research.

I was proud and honoured to be asked to take on the role of Chairman of CSIRO. Not only is its science a resource for this country but it is one of our nation's great Institutions. As my comments earlier would tell you, I place great store on the importance of such Institutions to our nation's future and their ability to guide and direct rather than just react to the changes taking place in Australia.

And while we will be endeavouring to bring stability to the Organisation, there will be plenty of tough decisions still to take. If Australia is to use its science to help create advantage, we have to recognise that we are going to have to make

choices about where our resources go. We cannot be in all areas of science and we will have to choose a few areas where we have the best chance of establishing a competitive lead in both our science and our business.

This will mean some areas will miss out. It will mean that some talented scientists will leave our shores in order to pursue careers overseas. That is something that we will have to accept, in the knowledge that we may be able to attract other leading scientists to our shores in the areas where we are recognised as being at the leading edge. That is just the ebb and flow of being part of the international community.

So, to sum up, Australia has more going for it in the 'flat earth' of the international marketplace than at first meets the eye. Its culture, institutions and its science give it a strategic advantage. They are not enough of themselves, but if Australia can continue its process of economic reform, there is every reason for optimism. If Australian science is the key to Australia's future, competitive Australian industry is equally the key to the future of Australian science.

Jack Cummins sought to foster exchange and interaction among scientists of different disciplines. If we expand Jack's model to include industry, we have the industry clusters described by Michael Porter and which, with economic reform are beginning to emerge in Australia. If we press on with that reform seeking outcomes, not process, those clusters and hence Australian science will have a flourishing future.

Ladies and Gentlemen, I hope that the scientific community will become a champion of continuing reform of Australia's economy, seeing its own and the national future in the success of those reforms. Then the key of science may well open the door of our nation's future.

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1997

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51321

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BIRCH, W. D., 1985. Calc-silicate rocks at Toolangi, Victoria. *Proceedings of the Royal Society of Victoria* 97: 1-18.

MACPHERSON, J. H. & GABRIEL, C. J., 1962. *Marine Molluscs of Victoria*. Melbourne University Press, Melbourne, xv+475 pp.

PARSONS, W. T., 1982. Weeds. In *Atlas of Victoria*, J. S. Duncan, ed., Victorian Government Printing Office, Melbourne, 122-125.

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PROCEEDINGS OF THE ROYAL SOCIETY OF VICTORIA

Volume 109, Number 1

CONTENTS

PROCEEDINGS

- RAYLENE COOKE, ROBERT WALLIS, ALAN WEBSTER AND JENNY WILSON
Diet of a family of powerful owls (*Ninox strenua*) from Warrandyte, Victoria 1
- MARGARET C. WARR
Regeneration of some forest and gully communities in the Angahook-Lorne
State Park (north-eastern Otway Ranges) 1-10 years after the wildfire of
February, 1983 7
- G. R. SHI AND SHU-ZHONG SHEN
A Late Permian brachiopod fauna from Selong, southern Xizang (Tibet), China 37
- THOMAS A. DIARRAGH
Gastropoda, Scaphopoda, Cephalopoda and new Bivalvia of the Paleocene
Pebble Point Formation, Victoria, Australia 57
- ALEXEI SMIRNOV AND TANIA M. BARDSLEY
Myriobrachys antarcticus sp. nov. (Apodida: Myriobrachidae), a new holothurian
species from eastern Antarctica 109
- KERRIE M. SWADLING AND IAN A. E. BAYLY
Different zooplankton communities in confluent waters: comparisons between
three marine bays in Victoria, Australia 113
- N. W. ARCHERD
Nomenclatural note 119

TRANSACTIONS

- Obituary—PATRICK SELLAR LANG 1
- Obituary—JAMES HAMEYN WILLIS iii
- FIFTY YEARS A GEOLOGIST xi
- J. E. CUMMINS OBE, 1997 Memorial Oration xiii